ENVIRONMENTAL AND BIOTIC INFLUENCES ON THE HOULOUT BEHAVIOUR OF **PHOCA VITULINA** (LINNAEUS, 1758) AND **HALICHOERUS GRYPUS** (FABRICIUS, 1791)

CLARENCE E. BUTTON

ENVIRONMENTAL AND BIOTIC INFLUENCES ON THE HAULOUT BEHAVIOUR OF *PHOCA VITULINA* (LINNAEUS, 1758) AND *HALICHOERUS GRYPUS* (FABRICIUS, 1791)

CLARENCE E. BUTTON

A thesis submitted in partial fulfillment of the requirements

for the degree of

Master of Science

Memorial University of Newfoundland

Department of Biology

1973

Abstract

Pinnipeds are the only group of mammals which exist in complete familiarity with the terrestrial and marine environments.

A colony of 423 Phoca vitulina and 82 Halichoerus grypus, legislatively protected in the Grand Barachois, Miquelon, were examined as to their behaviour permitting them to utilize both land and sea.

Haulouts of pinnipeds were descriptively and quantitatively examined by surveying the biota and topography of the preferred habitats. Fluctuations in meteorological and hydrographic parameters were correlated with variations in the position, number, species, sex and age composition of seal groups.

Sand or mud flat topography, isolation from mainland areas, proximity to migrant food sources, ambient air and sea temperatures and tidal variations were base site elements affecting seal behaviour. The crucial periods of parturition, mating and moult in the Harbour Seal are related to the resting aggregation of Grey Seals.

Acknowledgements

The author is indebted to Dr. John K. Ling for his supervision, encouragement and support of this study. The research was funded by National Research Council Grant A-5996 awarded to Dr. Ling.

The author is especially grateful to Dr. Cater W. Andrews for his considerate supervision, and with Dr. Charles C. Davis and Dr. J.K. Ling, for advice and constructive criticisms of the text.

Thanks are also expressed to: the Government of St. Pierre et Miquelon for permission to conduct the study in that territory; Mr. Graham Wood, Mr. Gordon Farrell, Mr. Tom Hynes and P.C.B. Oakum for assistance with the field research; M. Marcel Dagort and Mrs. Emaline Nicholle for their friendship and generous hospitality; Mr. C. Stephen Andrews for advice on computer programming; and Ms. Cathryn M. Noseworthy for encouragement and invaluable assistance in all phases of the work.

Table of Contents

List of Tables

List of Figures

Introduction

Behavioural research on the Pinnipedia has been primarily concerned with patterns of reproduction and moulting in the order (Backhouse & Hewer, 1957; Bartholomew, 1952; 1959; Bartholomew & Hoel, 1953; Bertram, 1940; Bishop, 1967; Boyd, 1957; Boyd & Laws, 1962; Boyd, Lockie & Hewer, 1962; Bychkov & Dorofeve, 1962; Cameron, 1967; 1969; 1971; Carrick, Csordas & Ingham, 1968; Csordas, 1958; Davies, 1949; 1952; Finch, 1966; Fisher, 1954; Harrison, 1960; Hewer, 1957; 1960; Hewer & Backhouse, 1960; Kenyon, 1960; Kenyon & Rice, 1959; Laws, 1956; Mansfield, 1958; Orr & Poulter, 1967; Peterson, 1965; Rand, 1955; 1967; Stirling, 1970; 1971a; 1971b; Venables & Venables, 1955; 1957). Such behavioural patterns have usually been described for small numbers of interacting individuals, either in their natural habitat, as above, or in confined experimental conditions (Finch, 1966; Schusterman, 1968).

These studies have described the individual behaviour patterns which are integral to whelping, nutritive and solicitous care of young, mating and moulting. Such crucial activities in pinnipeds occur annually in the above sequence during a short span of time varying from thirty to sixty days. Intraspecific and interspecific variations occur in the season or onset of the sequence of these activities (Backhouse & Hewer, 1957; Bartholomew, 1952; Bertram, 1940; Bigg, 1969a; 1969b; Bishop, 1967, Boyd, Lockie & Hewer, 1962; Cameron,

1969; Csordas,1958; Davies,1949;1952; Hewer,1960; Kenyon, 1960; Kenyon & Rice,1959; Ling,1969; Lugg,1966; Mansfield, 1958; Orr,1967; Orr & Poulter,1965;1967; Rand,1955;1967; Sergeant,1951; Stirling,1971a;1971b; Venables & Venables, 1955;1959; Wilke,1954).

These activities do, however, have one factor common to all species of the order. They are dependent on a suitable base site for their successful operation and completion (Bartholomew,1952; Bertram,1940; Bishop,1967; Boyd,1957; Boyd, Lockie & Hewer,1962; Cameron,1969;1971; Carrick et al.,1962; Davies,1949; Fisher,1954; Hewer,1957; Kenyon & Rice,1959; King,1964; Laws,1956; Lugg,1966; McLaren,1958a; Peterson,1968; Peterson et al.,1968; Rakhilin, 1968; Rand,1955;1967; Saundby,1960; Scheffer,1958; Sergeant, 1965; Venables & Venables,1955;1957). Perhaps due to their temperate and equatorial range restrictions, all species of the Otariidae, the sea lions and fur seals, habituate terrestrial base sites, which are often insular, with close proximity to the sea (Bartholomew,1959; Bartholomew & Hoel,1953; Bychkov & Dorofeev,1962; Csordas,1958; Kenyon, 1960; Kenyon & Wilke,1953; Orr,1967; Orr & Poulter,1967; Peterson,1965;1968; Peterson et al.,1968; Radford, Orr & Hubbs,1965; Rand,1956;1967; Scheffer,1958; Stirling,1970).

Members of the Phocidae, the true or hair seals, pursue their crucial activities on either terrestrial or glacial sites. Some pagophilic phocids are ice users

of necessity, since ice floes dominate all open water space and would prevent easy access to deep water feeding grounds from a terrestrial base (Bertram,1940; Chapsky, 1962; Fisher,1954; Lugg,1966; Mansfield,1958;1967b; McLaren, 1958b;1961a; Sergeant,1965; Stirling & Kooyman,1971). Other phocids, typically the more temperate Harbour Seal, Phoca vitulina, Grey Seal, Halichoerus grypus, and Southern Elephant Seal, Mirounga leonina, occupy terrestrial base sites where ice is seasonally present, but not in sufficient quantities to restrict animal movement (Bigg,1969a; Bishop, 1967; Boyd,1957; Boyd, Lockie & Hewer,1962; Cameron,1967; 1969;1971; Carrick & Ingham,1960;1962; Doutt,1942; Fisher; 1952; Hewer,1964; Laws,1956; Mansfield,1966;1967a;1967b; Peterson,1968; Scheffer,1958; Scheffer & Slipp,1944; Sergeant,1951; Sorenson,1960).

Amongst the species of the Pinnipedia, there is great variability in the duration that a species will occupy its base site habitat. The duration of site occupancy is reduced by the seal's performance of necessary aquatic functions, but is increased during the species' annual sequence of crucial activities related to reproduction and moult (Bertram,1940; Carrick et al.,1962; King, 1970; Peterson,1968; Scheffer,1958).

The major influence on time spent on the base site is the onus of food aquisition. Pinnipeds are unable to suckle their young in the water. The newborn is therefore dependant on the haulout site for this function.

(Backhouse & Hewer,1957; Bartholomew,1959; Bertram,1940; Carrick, Csordas, & Ingham,1962; Finch,1966; Fogden,1968; 1971; Kenyon & Rice,1959; Lockley,1966; Mansfield,1958; Orr & Poulter,1967; Peterson,1965; Peterson & Bartholomew, 1967; Venables & Venables,1955;1959). Adults of the species inhabiting areas where abundant food is proximate, need not leave the base site for durations as long as those species in relatively barren areas (Bertram,1940; Carrick et al.,1962; Fiscus & Baines,1966; Mansfield,1967b; McLaren,1958a; Rakhilin,1968; Rand,1959; Spalding,1964). Feeding time may vary from eight hours, (commonly observed in the Harbour Seal), three weeks (Cape Fur Seal, Arctocephalus pusillus,) or in excess of three months (Northern Fur Seal, Callorhinus ursinus)(Bertram,1940; Carrick et al., 1962; Ling,1970; Peterson,1968; Scheffer,1958; Kenyon & Wilke,1953).

Male seals of species with harem forming or territorial tendencies will fast for the duration of their lengthy occupancy of the base site during the breeding season. The Atlantic Grey Seal, the Southern Elephant Seal, as well as the great majority of the otariids are typical of the latter group (Bartholomew,1952; Bartholomew & Hoel,1953; Boyd, Lockie & Hewer,1962; Bychkov & Dorofeev,1962; Cameron, 1969;1971; Carrick, Csordas & Ingham,1962; Csordas,1958; Davies,1952; Hewer,1960; Kenyon,1960; Laws,1956; Peterson, 1965; Rand,1955;1967).

Promiscuously reproducing species as the Monk Seal, Monachus sp., Harbour Seal and Harp Seal, Pagophilus groenlandicus, are not restricted in this manner (Bishop, 1967; Fisher,1952; Kenyon & Rice,1959; Mansfield,1967b; Scheffer & Slipp,1944; Venables & Venables,1955;1957). There is very little evidence available to suggest that pinnipeds use water habitats for the performance of other socially significant behaviours, although aquatic courtship and copulation have been observed in the Weddell Seal, Leptonychotes weddelli, Hawaiian Monk Seal, Monachus schauinslandi, and the Harbour Seal (Cline, Sniff & Erickson, 1971; Kenyon & Rice,1959; Kooyman,1968; Venables & Venables, 1955;1957;1959). Other species of seals have been observed copulating in conditions of shore surf, but these incidents represent extensions of shore based activities and not aquatic behaviours (Backhouse,1969; Boyd, Lockie & Hewer, 1962; Cameron,1967; Hewer,1957; Lockley,1966). Nevertheless, the submarine calls of Bearded Seals, Erignathus barbatus, during the season of rut, have been interpreted as territorially important (Ray, Watkins & Burns,1969). Harp Seals are equally vociferous during rut and the synchrony of male Harp Seal aquatic activities suggests a group communication function (Button, unpublished data; Fisher, 1954; Terhune & Ronald,1972).

Mothers of precocial young seals are not restricted to the base site for pupping as those species with more altricial young. The white coats of the young Ribbon Seal, Histriophoca fasciata, Harp Seal, Grey Seal and Ringed Seal, Phoca hispida make them inefficient in the water, and restrict the dam with her stationary offspring to a small base site area (Fisher,1954; McLaren, 1958a; Peterson,1966; Scheffer & Slipp,1944; Siversten, 1941). Another influence on the time spent on the base site is the necessity for some pagophilic species, notably the Weddell Seal, the Ringed Seal and Harp Seal, to seasonally maintain breathing holes through the ice (Bertram,1940; Chapsky,1962; Freuchen & Salmonsen,1959; McLaren,1958a; Stirling,1969).

Aquatic play behaviour has been observed in the young of pinniped species, especially in maternal-young interactions. The maternal component of play can consist of correction and assistance in their initial efforts at swimming, predating and flight from danger, all of which are vital behaviours with great survival value. Such interactions between mother and young are usual until the pup is weaned, after which play activities are confined to discrete age groups of young (Bartholomew, 1959; Bishop,1967; Cline, Sniff & Erickson,1971; Finch,1966; Fogden,1968;1971; Lockley,1966; Peterson,1968; Peterson

& Bartholomew, 1967).

Evidence from diverse sources indicates that a base site may provide a variety of attributes which are functionally necessary to pinnipeds. The attributes suggested as being important to seals are: suitability of surface for ambulation, protection from aquatic enemies or terrestrial predation, places of rest, proximity to food abundance, suitability for the performance of reproductive and moulting activities, loci for the physiological formation of body nutrients or solar dependant vitamins, protection from inclement weather or sea conditions and exposure to desirable meteorological conditions.

The number of these attributes which a pinniped requires for survival varies among species. Some species, such as the Grey Seal, seem flexible in their choice of base site habitat, and utilize any available stratum. This species parturates and mates on sandy dunes of Sable Island, on the rocky shores of the Outer Hebrides and on islands in the Gulf of St. Lawrence (Boyd, 1947; Boyd et al., 1962; Hewer, 1957; Mansfield, 1966; 1967a; 1967b). Harbour Seals, however, have definite preferences for specific types of base locations. Three Phoca vitulina subspecies, vitulina found in the North Atlantic, concolor in the West Atlantic and richardii in the Northeast Pacific, all prefer base habitats presently or historically of estuarine design (Bigg, 1969a; Bishop, 1967; Boulva, 1972; Fisher, 1952;

Mansfield,1967a;1967b; Merdsoy,1973; Venables & Venables, 1955;1957; Wilke,1954). Most terraphilic phocids are found in association with sandy atolls or lagoons such as the Hawaiian Monk Seal or Northern Elephant Seal, the Harbour Seal and Grey Seal (Bartholomew,1952; Bishop, 1967; Butler & Udvardy,1966; Fisher,1952; Kenyon & Rice, 1959; Mansfield,1966; Van Bemmel,1956).

Pagophilic phocids in both arctic and antarctic regions exhibit species-specific glacial distributions. Within a species, there is little variation in the type of ice utilized as a base site. Weddell Seals in the Antarctica and Ring Seals in the Arctic are commonly found on fast shore ice miles from the flow perimeter (Bertram,1940; McLaren,1958a;1961a; Stirling, 1969). The arctic group of Harp Seals, Bearded Seals, Hooded Seals, Cystophora cristata, and Ribbon Seals, with their antarctic counterparts, the Crabeater Seal, Lobodon carcinophagus, the Ross Seal, Ommatophoca rossi, and the Leopard Seal, Hydrurga leptonyx, are chiefly inhabitors of thick sea ice between migratory periods (Bertram,1940; Chapsky,1962; Dunbar,1949; Laws,1953; Lindsey,1938; Mansfield,1967b; McLaren,1958b; Olds,1950; Peterson,1966; Stirling & Kooyman,1971; Siversten,1941).

Members of the family Otariidae prefer boulder or slab base habitats. (Kenyon,1960;1962; Orr, 1967; Peterson,1965;1968; Peterson et al.,1968; Rand, 1967; Scheffer,1958). This family is generally more

pelagic than the phocids, utilizing the base site regularly and continuously only at times of reproduction (Bychkov & Dorofeev,1962; Csordas,1958; Fiscus & Baines,1966; Kenyon & Wilke,1953; Orr & Poulter,1967; Rand,1955; Stirling,1970; Siversten,1953).

The killer whale, Orcinus orca, and a variety of large sharks are the only known aquatic enemies of pinnipeds (Bigelow & Shroeder,1953; Slijper,1962). Groups of these predators of seals patrolling land masses have been correlated with pinnipeds in waters nearby emerging from the water onto land (Norris & Prescott,1961). Since base sites are present in only a small portion of the pelagic seals' aquatic range, hauling out onto land must provide only limited protection from aquatic predators. There are few known terrestrial predators of pinnipeds, probably due to the seal's choice of inaccessible promontories and beaches, for, despite the seal's ferocity in self defence, the author has observed an Alsatian dog kill a one year old Phoca vitulina while the latter was retreating to the water. Packs of feral canids thus probably have the potential for predating available pinniped stocks, hence, choice of the appropriate base site is probably instrumental in preventing or reducing terrestrial danger. The only pinniped imminently susceptible to terrestrial predation by Polar Bear (Thalarctos maritimus), the Ringed Seal, has developed

ancillary camouflage procedures in forming subnivean dens for the purpose of parturition (Fisher,1950; McLaren,1958a).

A base site may provide a place of rest for the pinniped. However, many seals, sea lions and fur seals have been observed sleeping or otherwise resting while in the water (Lockley,1966; Rand,1967; Scheffer, 1958). Thus a solid stratum is not a necessary, but a common, requisite for rest. Since diving inhibits the digestive process of pinnipeds, resting, at sea or on land, may facilitate this process (Elsner et al.,1966; Irving et al.,1942; Scholander,1940; Scholander et al.,1942; Van Critters et al.,1965). Terrestrial rest, however, would only facilitate intestinal digestion, since seals typically haulout to the base site with empty or near empty stomachs (Fiscus & Baines,1966; Myers,1959; Sergeant, 1973; Spalding,1964; Wilke & Kenyon,1952;1954).

Evidence that a base site is advantageous because of its proximity to the pinniped's food source is indeed scanty, and is only pertinent to those animals exhibiting a site tenacity or relatively sedentary existence, such as the Harbour Seal, Walrus, Odobenus rosmarus, the Grey Seal, the Ringed Seal and the California Sea Lion, Zalophus californianus (Fisher,1952; Imler & Sarber,1947; Scheffer & Slipp,1944). Carrick & Ingham (1966) have found that the South Pacific islands

used as regular base sites by the Southern Elephant Seal, lie in the subarctic belt that is continually food rich, although varying seasonally in ocean depth. The aquatic initiation of young Elephant Seals coincides with the peak surface availability of their known food items (copepods, chaetognaths, euphausiids and amphipods) during the southern spring. McLaren (1961a;1961b) has supplied evidence that adequate food stocks abound near the fast ice habitat of Ringed Seals in the eastern Canadian Arctic. Chapsky (1962) suggested that food availibility combined with suitable ice conditions are the requirements of Harp Seals in the White Sea reproductive and moulting areas, and other authors have inferred these attributes to be necessary to Walrus aggregations (Burns,1970; Fay & Ray,1968).

That pinnipeds use base sites for reproductive activities of parturition, courtship, and copulation followed by moulting has been previously documented in the text, as have the exceptions to this generality. Three types of haulout have been described in Mirounga and Halichoerus according to their function. These types include breeding, moulting and resting haulouts, the former two characteristically utilizing areas of the base site above high water level, the third type occupying regions exposed by low tides (Bartholomew,1942; Carrick et al., 1962; Waters,1965). Haulout loci are integral to post

parturant pup vitality, even in the most precocious of pinnipeds, the Harbour Seal. No seal has achieved the behavioural mechanisms permitting cetacean type aquatic births (Caldwell & Caldwell,1966; Caldwell, Caldwell & Rice,1966; Slijper,1962; Tavolga & Essapian,1957).

Two dimensional base sites (i.e. terrestrial or glacial) are usually prerequisite to the maintenance of territorial or polygamous breeding habits, but not for actual copulatory activities. Nevertheless, it would seem advantageous for the Mirounga and Halichoerus genera to alter the locus of breeding to the aquatic environment, their aquatically adapted size being somewhat an onus on land (Bartholomew,1952; Hewer,1957; Laws,1956; Mansfield, 1958; Nikulin,1947).

Aerial moulting is universal throughout the Pinnipedia, but not all members of the order relegate themselves exclusively to the land during this period. A reluctance to enter the water has been noted generally for P. vitulina (Bishop,1967; Fisher,1952; Scheffer,1958), and specifically for the Hawaiian Monk Seal (Kenyon & Rice,1959) during the moult period.

Increase in haulout numbers during the seasons of reproduction and moult have been observed in all accessible species and is more pronounced in gregarious species (Bertram,1940; King,1964; Peterson,1966; Scheffer, 1958). Gregariousness during parturition and breeding

is explained by the choice of suitable pupping and copulation sites and the necessity of male-female proximity. The incentive for congregating during moulting, and outside these crucial periods, has not been clearly defined. The moulting aggregations of Mirounga sp. are large groups with reduced distances between individuals, and unique among seals, positive thigmotaxis (Carrick et al., 1962; Bartholomew, 1952). Increased irritability, with concomitant aggression, and, in all but Monachus sp., a certain amount of scratching and rubbing of the affected body surfaces are prevalent during moult (Kenyon & Rice, 1959).

Several phocids, including Monachus and Mirounga, fast during the moult as well as during breeding haulouts, but this is more generally the case in the Otariidae (Bartholomew, 1952; Bartholomew & Hoel, 1953; Csordas, 1958; Kenyon & Rice, 1959; Ling, 1970; Orr & Poulter, 1967; Peterson & Bartholomew, 1967). In species that observe these fasts, there is commonly a period of time between reproductive activities and moulting, when restorative feeding occurs (Bartholomew, 1954; Carrick et al., 1962; Ling, 1965; 1970; Sergeant, 1965; 1973; Siversten, 1941). Pinnipeds that are known to feed during reproduction, such as the Harbour Seal, and all but parturant females in the genus Monachus, need less recuperative time between reproduction and moult (Ling, 1970; 1972; Venables & Venables, 1955).

Photoperiodicity has been suggested as an

ultimate initiator of moulting, however, other factors modify this parameter. The occupation of moulting base sites may vary with the sex and age class of the same species. Nulliparous and primiparous Mirounga sp. seem to moult at the same time as juveniles, whereas adult males and multiparous females delay the moult for six weeks of post-reproductive feeding (Carrick et al.,1962; Ling,1965). A nutritional prerequisite for moulting is thus suspected.

Even considering geographical range differences, pinnipeds in both hemispheres moult in the period from early spring to mid-autumn, indeed the months affording greatest solar radiation (Ling,1970). This solar influence has been suggested as important in raising epidermal and dermal temperatures to the 30°C. level necessary for optimal growth and repair (Feltz & Fay,1967). Trichial growth in the dermis may correspondingly be ambient temperature dependant. Seals to the South of the equator moult in a more restricted time period from December to May, the southern summer and autumn. This timing may reflect the end of weaning during a season when the young seals' aquatic habitat is nutritionally appropriate. In this case, the beginning of moult would be merely a step in the ongoing hormonal processes of the pinniped crucial period.

Aggregations of seals are known to occur

outside the crucial periods of reproduction and moult. At least one author has suggested that these aggregations occur more as a result of a site preference than a pronounced gregarious tendancy (Kenyon & Rice,1959). Such aggregations are susceptible to changes in size and location due to inclement weather conditions of surf and wave action on exposed base sites (Carrick et al.,1962; Hewer & Backhouse,1960; Kenyon & Rice,1959; Rand,1967). These same conditions, which have little effect on seal adults, can induce mortality in pups. Weddell Seals, Grey Seals, Walrus and Northern Fur Seals withdraw into the sea or huddle together in winter storms (Bartholomew & Wilke, 1956; Fay & Ray,1968; Smith,1965; Waters,1965), whereas more equatorial species such as the Southern Elephant Seal, the Monk Seal, the Cape Fur Seal and the Harbour Seal greatly prefer the land (Bishop,1967; Carrick et al., 1962; Kenyon & Rice,1959; Rand,1967). Wind is an excessive cooling factor in the former case and causes intolerable oceanic disturbance in the latter. Some pinnipeds, such as the Cape Fur Seal and the Harbour Seal, during heavy rain or thunder, and the latter species when fog conditions and negligible winds create a heat canopy effect forsake the land. (Rand,1967).

Temperature through solar radiation is probably the important environmental parameter around which the seal's ecology revolves. Pinnipeds contend with greater extremes of air temperature than water temperature. Water has

higher specific heat values, being less variable or easily modified by atmospheric temperatures (Butler & Udvardy,1966; Fay & Ray,1968; Irving,1969; Peterson et al., 1968; Rand,1967; Ray & Smith,1968; Ray & Fay,1968, Vaz Ferreira,1956).

All pinnipeds have anatomical and physiological modifications enabling endurance of the aquatic heat sink. These adaptations include insulative blubber thickness, the "green house" effect known to occur with the inward reflecting dry natal fur of young seals, extensive vascularization of the dermis and its voluntary dilation or constriction as heat retainers or dispensers, countercurrent systems of heat exchange to the periphery of the animal, especially appendages, cardiac and respiratory rate control, thus decreasing or increasing metabolic heating (Davydov & Makarova,1964; Elsner & Kenney,1966; Scheffer,1958; Scholander & Schevill,1955; Scholander et al.,1950a; 1950b; Tarasoff & Fisher,1970). These adaptations, even though their mechanisms are also used for cooling, may in the atmosphere, prevent sufficient body heat dissipation (Bartholomew & Wilke,1956; Harrison & Kooyman,1966; Irving & Hart,1957; Laws,1956; Kooyman,1968; Ray & Fay,1968; Scholander et al.,1942). In this circumstance, behavioural mechanisms for body temperature reduction are used. The genera Callorhinus, Arctocephalus and Zalophus exhibit behavioural thermoregulatory aids,

by seeking shade and moisture beneath rock outcroppings (Bartholomew & Wilke,1956). Hawaiian Monk Seals make wallows in moist sand and attain the shade of bushes above the beach, or as genera Mirounga, Otaria and Odobenus, return to the water for cooling purposes (Bartholomew, 1954; Butler & Udvardy,1966; Carrick et al.,1962; Fay & Ray,1968, Kenyon & Rice,1959; Laws,1956; Vas Ferreira & Palerm,1961; White & Odell,1971).

Mirounga, Monachus and Arctocephalus species also cool their solar-facing, dorsal surfaces by flipping cool damp sand onto their backs (Kenyon & Rice,1959; Laws,1956; Rand,1967; Vas Ferreira & Palerm,1961; White & Odell,1972).

Increased individual distances have been noticed in Odobenus and Arctocephalus species under heat stresses approaching their upper thermal tolerances. Walrus, huddle together to reduce exposed surface area during extreme cold (Fay & Ray,1968; Vas Ferreira,1956; 1959).

Strong correlations between temperature and seal gregariousness have also been found in the Harbour Seal (Ling & Button,1972). These observations constitute the only available records of a thermal effect on gregariousness in the order.

Pinnipeds also contend with extremes at the

cold end of ambient temperature range with behavioural thermoregulatory aids. Predictably, the Weddell Seal of the extreme South orients itself at right angles to incident solar radiation, when atmospheric conditions are clear and permit this heating activity (Ray & Smith,1968; Smith,1966). White-coated Harp Seal pups prefer resting sites near vertical ice rafts where solar heating may be reflected to larger areas of the animals' surface (T. Øritsland, personal communication).

The distribution of two species has been correlated, although by implication, with a definite range of oceanic surface temperature. Callorhinus sp. and Arctocephalus pusillus show preferences for water temperatures between 12° and 16°C. (Kenyon & Wilke,1953; Rand, 1959), however, whether this indicates a thermal preference or an adherence to an abundant pelagic food source is unknown.

Circadian rhythms are known in the Pinnipedia, and should be considered when examining the seal's requirements for a base site. Aquatic activity is greatest at night in Leptonychotes, Eumetopias jubata (Steller Sea Lion), Monachus, Arctocephalus foresteri (New Zealand Fur Seal), and Phoca vitulina in insular habitats, however daylight feeding is common in Arctocephalus pusillus (Boulva,1972; Butler & Udvardy,1966; James,1972; Mathisen & Lopp,1963; Smith,1965). Odobenus sp. exhibit a bimodal

haulout number variation, the peaks occurring in early morning and early afternoon (Fay & Ray,1968).

Other species; such as Halichoerus grypus and Phoca vitulina, in estuarine habitats, emerge from the water in total dependency on tidal conditions, and in greatest numbers during ebb and low tide (Bishop,1968; Boyd,1963; Fisher,1952; Harrison,1960; Venables & Venables, 1955; Waters,1965). Halichoerus shifts the relationship during the periods of reproduction and moult when more animals leave the beaches at ebb tide than at any other time of the diem (Cameron,1970).

On the basis of the data reviewed here, then, an important aspect of the biology of the Pinnipedia is the utilization of and dependence on two totally different environments, aquatic and terrestrial. However, the haulout behaviour of seals has only been descriptively examined and attributes of either the terrestrial or aquatic habitat to which seals respond, or which may initiate haulout behaviour, have not been sufficiently studied.

The two phocids present throughout the year in waters off Newfoundland, Phoca vitulina and Halichoerus grypus, seem to utilize specific land bases from which to operate their marine feeding forages, probably as a function of their latitudinal dispersion in the northern hemisphere and their terrestrial parturition. The preferred

terrestrial habitats of both species have been documented; the Harbour Seal inhabits mainly sand-lagoon situations and the Grey Seal is usually found in rocky insular habitats. Beyond annual counts on certain British islands and incidental information pertaining to the reproductive season, no quantitative ecological investigations of the haulout phenomenon have been reported. The present investigation was an attempt to provide this information.

More specifically, the present study, utilizing a large aggregation of Phoca vitulina concolor and Halichoerus grypus, attempted to investigate:

1. the environmental and biological variables, that appeared important, and to which seals may respond
2. the nature of the seals' responses and
3. the quantitative importance of each variable to the seals' ecology.

Description of the Study Area

The French Territory of Saint-Pierre and Miquelon consists of an archipelago of several small islands and islets some 20.93 kilometers from the southern tip of the Burin Peninsula of Newfoundland (Fig.1). There are three main islands; Saint-Pierre, Langlade and Miquelon. A narrow isthmus has formed only in the last 200 years to join Langlade with Miquelon (Rannie,1968) which lie about six miles apart. Prior to the formation of this isthmus, sailing vessels sailed between these two islands and shipwrecks near the passage were focal points of sand consolidation for its closure (Dagort, personal communication). The principal area of the present study was centred on a series of sand banks which are exposed at low tide in the Grand Barachois at the southern end of Miquelon (Fig.2 & 3).

The Grand Barachois is roughly the shape of an equilateral triangle with sides 4.25 km. in length. It opens to the sea at the southeastern corner through a narrow channel, la Goulet de Langlade. Considerable tidal currents, to seven km. per hour, result from the tidal flow of large volumes of sea water through la Goulet de Langlade and other narrow channels within the barachois. Tidal ebbing exposes extensive areas of sand bank which are covered at high tides to a depth of one to three meters. At spring high tides, sand banks in the Grand Barachois are covered by a minimum of two meters and a maximum of

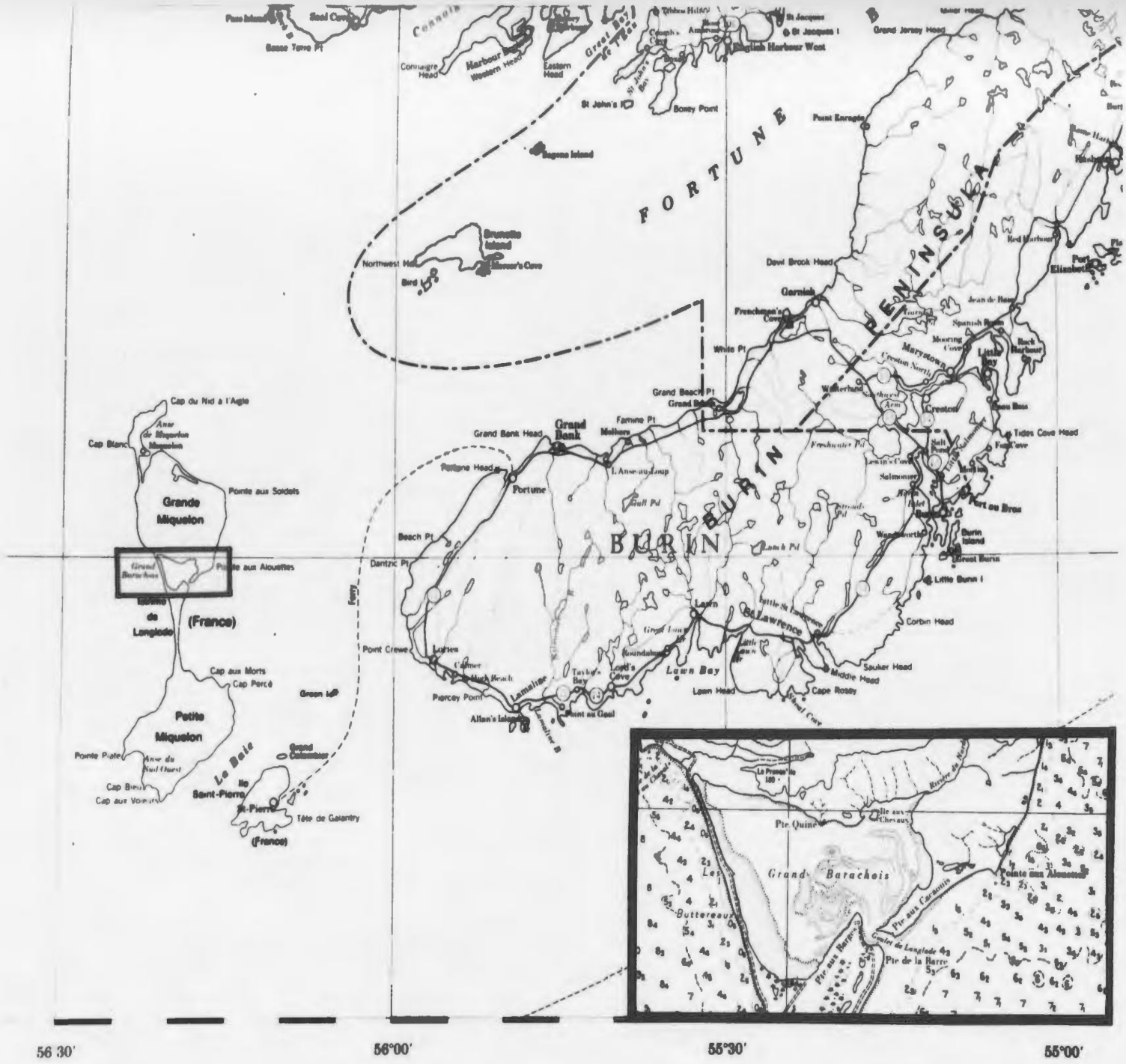

Fig. 1 Map of Saint-Pierre et Miquelon

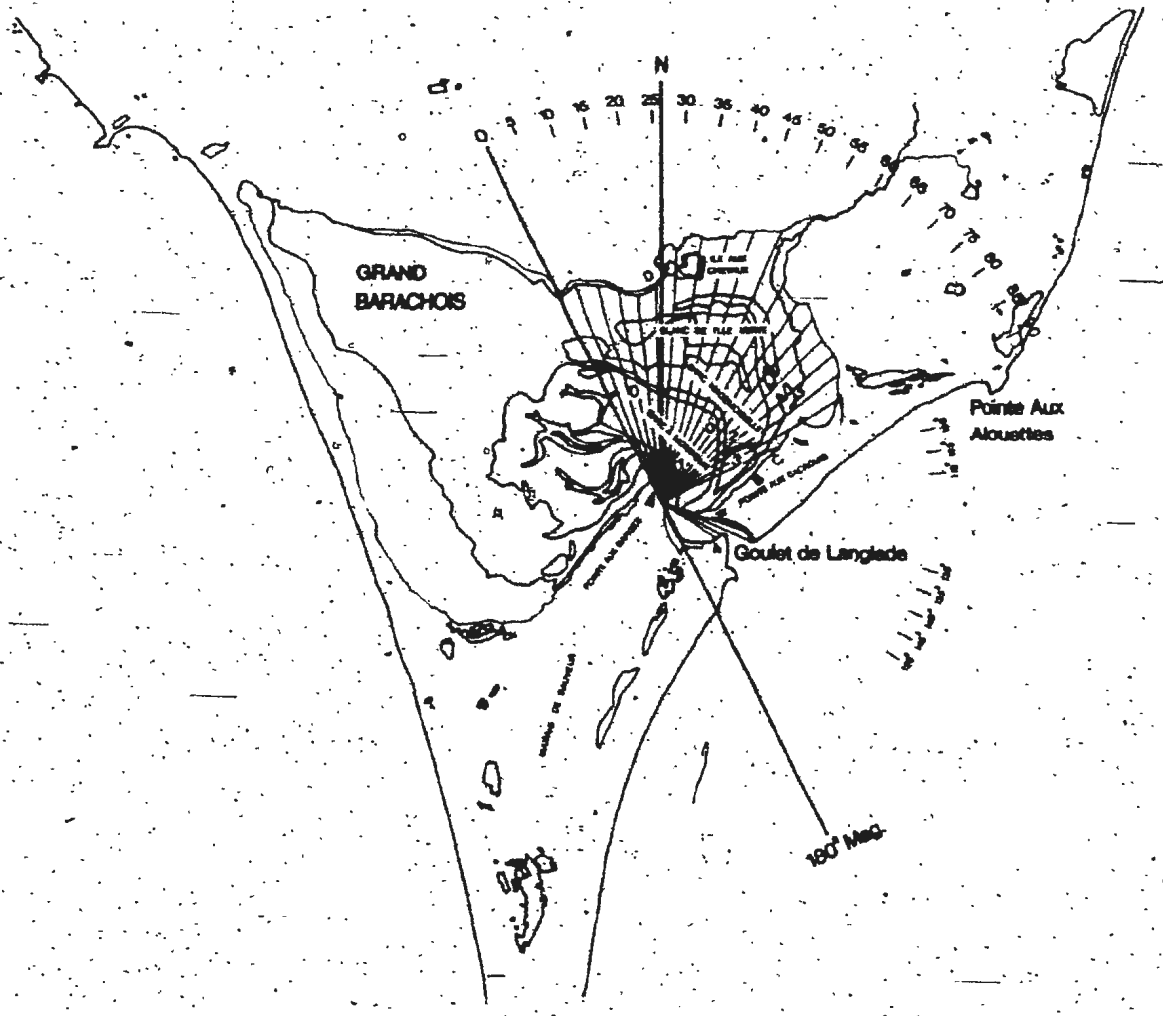

Fig. 2 The Grand Barachois Showing Study Site Locations and Seal Haulout Locations

Fig. 3 Aerial View of the Grand Barachois Study Site

four meters of oceanic inflow. During spring low tides, the channels scoured by tidal action are at a maximum depth of three and one-half meters, the deepest troughs being near la Goulet de Langlade. Tidal extremes within the Barachois are never as great as those in the nearby sea. The narrow channel joining this island lagoon with Fortune Bay restricts tidal flow, retaining a water level in the barachois higher than that of the oceanic low tide. The reverse is true at high tides and the same mechanism causes a 35 minute time lag between the tidal extreme of the sea and that of the lagoon. The position of the sand banks changes minimally from year to year. The major alterations, resulting from storm and wave action or winter ice dams, occur near la Goulet de Langlade.

The shoreline of the Grand Barachois consists of clean golden sand or pebble beaches cut by several small streams arising from marshes to the South and 200 m. altitude hills to the North. The fresh water runoff into the lagoon through these streams is usually quite minimal. Rarely, heavy rain may cause the typically crystaline barachois waters to become cloudy or brown and decrease the salinity of effluent tidal currents. The marine inhabitants of the Grand Barachois, shown in Table 1 and Fig. 4, indicate a typical estuarine setting.

Low-lying sand dunes, up to 15 m. in height, and grassy plains immediately surround the barachois.

Table 1

List of Marine Species of the Grand Barachois

Phylum	Species	Code*
Phaeophyta	Agarum cribosum	a
	Fucus vesiculosus	
	Desmerestia aculeata	
	Dictyosiphon foeniculaceus	
Rhodophyta	Porphyra umbilicalis	
Phanerogama	Zostera marina	z
Mollusca	Placopecten magellanicus	p
	Mytilus edulis	e
	Mya arenaria	m
	Littorina littorea	
	Littorina saxatilis	
	Thais lapillus	
	Lunatia heros	
	Acmaea testudinalis	
Annelida	Nereis pelagica	
Echinodermata	Strongylocentrotus dröbachiensis	
Arthropoda	Homarus americanus	h
	Cancer irroratus	c
	Pagurus longicarpus	

*See Fig. 4 for distribution of coded species.

Table 1 - (Cont'd)

Phylum	Species	Code
	Idotea baltica	
	Gammarus lawrencianus	
	Crangon septemspinosus	
	Balanus balanoides	
Vertebrata	Raja erinacea	r
	Charcharinus obscurus	
	Gadus morhua	g
	Microgadus tomcod	
	Myoxocephalus octodecemspinosus	o
	Myoxocephalus scorpius	s
	Pleuronectes americanus	
	Mallotus villosus	v
	Osmerus mordax	
	Salvelinus fontinalis	f
	Scomber scombrus	b
	Gasterosteus aculeatus	
	Phoca vitulina	x
	Halichoerus grypus	y

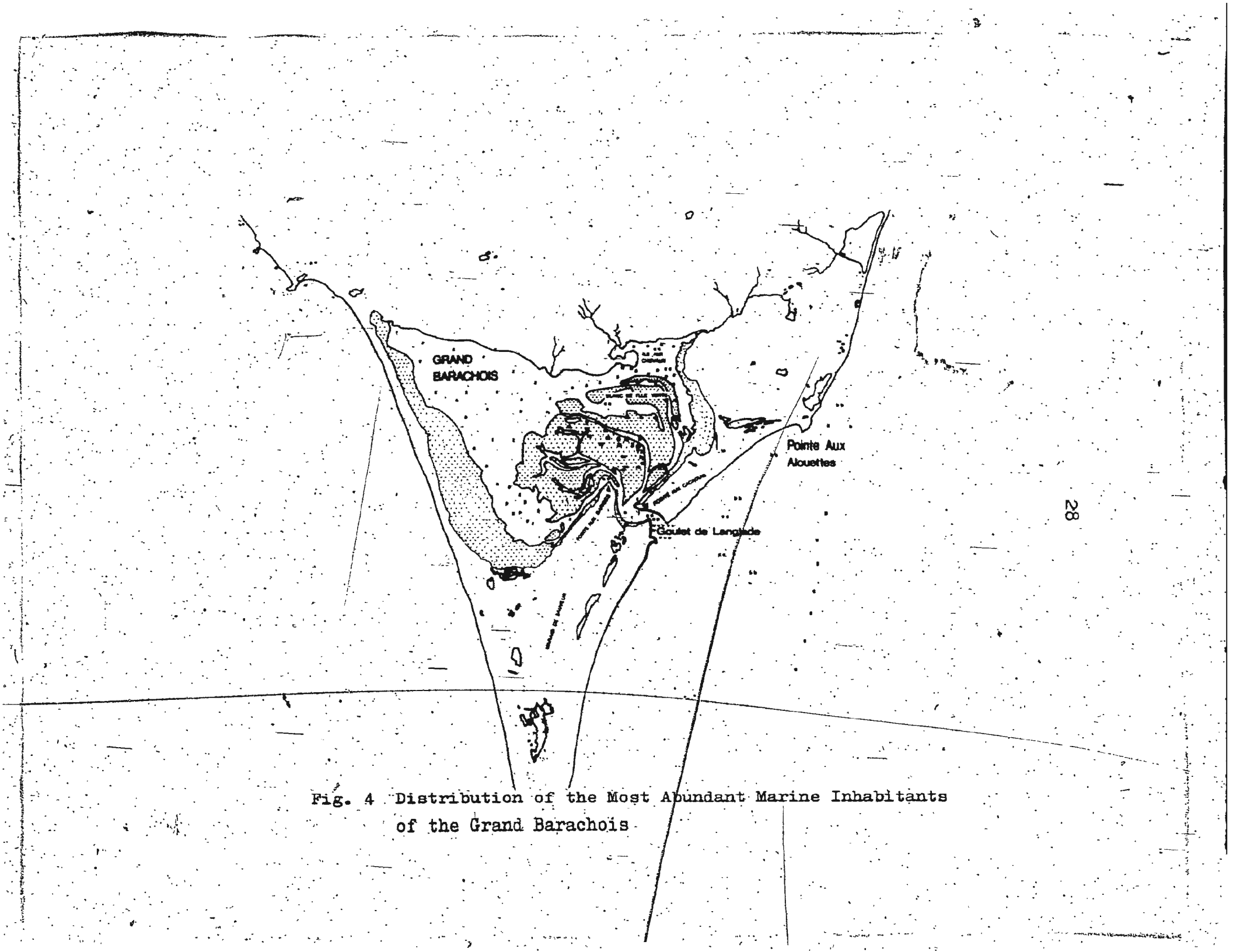

Fig. 4 Distribution of the Most Abundant Marine Inhabitants of the Grand Barachois

The vegetation of these areas consists entirely of sea shore wildflowers (e.g. Lathyrus japonicus), typical dune grasses (e.g. Ammophila breviligulata) and, rarely, woody shrubs (e.g. Alnus rugosa).

The marsh areas to the South and Northeast of the barachois are of interest in that they provide rest and feeding stops for several species of migrating game fowl, and nesting areas for Black Duck, Anas rubripes, and Wilson Snipe, Capella gallinago (Peters & Berleigh, 1951; Tuck & Borotra, 1972).

Feral horses, Equus caballus, which originated from farm stock about 30 years ago, have maintained a steady population level of 40-50 animals in the area. Other terrestrial mammals found on the isthmus are: Rattus norvegicus, Lepus americanus, Odocoileus virginianus and Vulpes vulpes.

The type of marine environment of the Grand Barachois provides the habitat for the Harbour Seal and occasionally for the Grey Seal around the south coast of Newfoundland (Templeman, Squires & Flemming, 1957). The isthmus between the islands of Miquelon and Langlade is uninhabited by humans excepting the inhabitants of one summer cottage three km. from the barachois. In addition, there are two shelters at Pointe aux Barges that are occasionally used by fishermen. The Grand Barachois is reasonably isolated, disturbed only in early July by fishermen collecting mussels for bait and in late September

by wildfowl hunters. The Grand Barachois itself is a legislated conservation site and firearms are not permitted in its proximity.

Other areas containing small seal aggregations during the mid summer each year were; Trous Loup Marin and tidally exposed rocks near Pte. du Chapeau, Miquelon; Little Green Island and Lories (Pt. May Barachois) on the south coast of Newfoundland (Table 2).

Trous Loup Marin and Lories offer similar habitats. Both are small tidally influenced lagoons, Lories being the larger. Trous Loup Marin on the West of Petite Miquelon has a maximum depth of 10 m. and is surrounded by 10-20 m. embankments with a beach on the landward end. Some rocks are uncovered during falling tides and these, with the inner rock beach, were the occasional resting base sites for P. vitulina.

Lories is a much shallower lagoon (6 m. depth) on an exposed and low-lying peninsula. The lagoon itself is the shape of a .75 km. long oval with a channel to the sea opening on the southwest side. Many large flat or irregular topped rocks protrude above the surface at low tide and on them P. vitulina were observed.

Little Green Island has an area of approximately 1500 sq.m. and is situated 6 km. to the Southwest of Lories, and 6.44 km. to the Northwest of St. Pierre. It arises rather sharply from the sea to a partially grassy plateau some 4-5 m. above mean sea level. On this plateau and on

Table 2

List of Areas near Miquelon Populated by *Phoca vitulina* and Observed Numbers in each Location.

Location	Number of Animals
Grand Barachois	423
Trous Loup Marin	28
Rocks near Pte. du Chapeau	15
Little Green Island	52
Pt. May Barachois (Lories)	34

a jagged, wave washed rock beach to the South, a small aggregation of P. vitulina was sighted.

Tidally exposed rocks, near Pte. du Chapeau to the Southeast of Miquelon village, have an area of about 100 sq. m. These rocks are almost flat topped and covered on their seaward edges by Fucus sp. and Agarum sp. Other than these plants, they are devoid of vegetation and are awash even at low tide in high seas.

Due to the difficulty of travelling to these four isolated seal base sites, the only information on the numbers of seals utilizing these areas was obtained during one visit to each. It is thus not known if P. vitulina uses these sites for breeding purposes. Since all visits were of necessity made on calm days, it is also not known whether these sites are occupied during stormy weather nor the extent to which they are used.

H. grypus were not observed at any of these sites.

Methods and Materials

Data were collected during the months of June-September, 1971 and May-September, 1972.

Observations of the seals at the Grand Barachois were taken at hourly intervals during all daylight hours of the study period. Irregular observation intervals were frequently necessary due to persistent heavy fog conditions and occasionally due to necessary absences of the author from the study site.

The major observation site was at the Northern end of the fishermen's cabins at Pointe aux Barges (See Fig. 2, A & Fig. 3). Other ancillary observations were made as required from a variety of other locations shown in Fig. 2 (B,C,D). From observation point A, eight environmental and seven biotic variables were recorded for each hourly observation. These were:

Environmental variables.

Time. This variable was recorded in Atlantic Standard time using a 24 hour Schultz clock which was checked daily with AM radio broadcasts of Greenwich Mean time.

Air temperature. A -10 to 110° Centigrade mercury thermometer was used to record temperature. It was positioned at observation site A, 2 m. from the ground, so that it was continually hidden from direct solar heating but exposed to all available air currents.

Water temperature. A -10 to 110° Centigrade

mercury thermometer was used to record water temperature. The thermometer was immersed in the barachois water to a depth of one meter for two minutes. It was then brought to a depth of two centimeters and read immediately.

Wind speed minimum and maximum. Wind speed was recorded using a 0-80 m.p.h. Wilh. Lambrecht K.G. meteorological anenometer which was fixed at a height of four meters above mean sea level and 20 meters from the fishermen's cabins at Pointe aux Barges to reduce geographic influences. This apparatus was observed for one minute at each hourly reading, and the maximum and minimum wind speed within that interval was recorded, and converted to the metric system.

Cloud cover. Cloud cover was subjectively determined by the author by a 360° scan of the available horizon and a vertical scan from North to South. It was recorded to the nearest ten percent.

Tide height. Tide height was determined at the study site by tabular data taken from Canadian Hydrographic Service Tide Tables for 1971 and 1972. The closest tide reference point to the Grand Barachois was Saint-Pierre. To determine the time differential between tidal extremes at the reference port and the Grand Barachois, a floating flourescent painted board was anchored in three meters depth near the south shore of la Goulet de Langlade. The board was watched closely at tidal extremes to determine

when tidal flow direction changed. Hence the precise time of tidal extremes at the Grand Barachois was found to constantly lag behind those at Saint-Pierre by 115 minutes. Tide heights in feet were then taken directly from the reference point tide table information at times corrected to the study site, and converted to meters.

Tide status. This variable described the direction of tidal change at the time of observation. The four classes used to describe tide status were rising, falling, high or low tide. The flourescent board described previously was used to determine the appropriate class.

Biotic variables.

Haulout location. Five discrete terrestrial bank locations were used for hauling out by seals in the Grand Barachois at some time during the study period. These stations were coded 0-4 inclusive and their positions are shown in Fig. 2 & 3.

Group span minimum and maximum. From observation point A, the extreme edges of separate groups of seals were sighted through a 30 x T.H.S. #460 theodolite. This instrument provided the angle from magnetic North of any point on the seal inhabited sand banks, which described arcs around observation point A. These angles magnetic were recorded for the easternmost and westernmost extremes of all seal groups visible. The angle of the westernmost point of a seal group was termed the group span minimum

angle and the angle of the easternmost point of the seal group was termed the group span maximum angle. Groups of seals were defined as those collections of animals which exhibited a separate and discrete aggregation with a subjectively homogeneous density. A compact aggregation of seals was differentiated from a loosely scattered number of seals nearby. A compact group of Halichoerus grypus was differentiated from compact groups of Phoca vitulina, although the former species group was well within the confines of the latter. The two species were always recorded separately.

Group number. This variable was recorded as the number of seals within the group minimum angle and group maximum angle.

Group composition. The categorization of groups of seals according to age, sex and species at great distances was initially unreliable (Ling & Button, 1973). Competence in these types of classification was achieved by viewing the animals from afar, then approaching the same animals to confirm the results of long distance observation. If the sex, species and age composition of any group was in doubt, such as in conditions of fog, blowing sand or light refraction through convection currents across sand banks, the observer boated to stations B to D to obtain short distance observations through 7 x 50 Tasco binoculars. This was done within the hour interval between sightings

from observation station A.

Species. Seal groups were classified according to species, Phoca vitulina or Halichoerus grypus. These species were differentiated on the bases of size, cranial conformation and profiles, and coat colour (See Doutt,1942; Peterson,1966; and Table 3).

Sex. Halichoerus grypus, the Grey Seal, was easily sexed since it is obviously sexually dimorphic (Table 3). Phoca vitulina, the Harbour Seal, is not sexually dimorphic, although males tend to be larger than females. Sexing this species was performed by viewing the presence or absence of the penile aperature or vulva. When these structures were not visible through the theodolite or by short distance observation, the group was not classified according to sex. Groups were classified according to four sex categories; male, female, male and female, and undetermined.

Age. It was not possible to collect many animals in the study area for reasons of excessive disturbance and French regulations prohibiting the sacrificing of seals. Hence the segregation of seals into separate age classes was not possible by the dental ageing procedures of Laws (1952,1962), Mansfield & Fisher (1960) and Bishop (1967). Both species were classified as belonging to one of three age classes based on function; pup, juvenile and adult. Pups were obvious until their third month of age by their small size and until weaning by their proximity to the dam.

Table 3

Phenotypic Differences between *Phoca vitulina* and *Halichoerus grypus* and between Sexes of Each Species.*

Measurement		*P. vitulina*	*H. grypus*
Total length (in cm.)	male	1350–1800	1600–3600
	female	1350–1800	1500–2100
Skull length (in cm.)	male	162–222	260–330
	female	162–222	208–265
Skull width (in cm.)	male	100–128	140–200
	female	100–128	120–140
Weight (in lbs.)	male	130–300	350–800
	female	100–160	250–600
Coat colour	male	varies in amounts of dark brown spots on yellow to fawn, darker above than below.	predominantly black with some white spots.
	female	same as male	predominantly white with black spots.

*Taken from data reported by Peterson(1968) and Hewer & Backhouse(1959).

Adults were defined as capable of breeding in that calendar year and juveniles as the class within one year of age and adult age. These age classes were determined on the basis of size in P. vitulina, standard length increasing significantly only to the breeding age of four years (Bishop, 1967). A small number of teeth were collected from all age classes of the Harbour Seal as part of a broader study to corroborate the size-age correlation noted by Bishop (1967). Pups of the Grey Seal were never observed at the Grand Barachois. Juvenile and adult Grey Seals were differentiated on the criteria of relative size and skull conformation. These criteria were confirmed as valid by observations of breeding H. grypus on Sable Island (Ling & Button, 1972). From the three age classes, seven combinations of age groups were possible. A single discrete group of animals could thus be observed to contain: 1. pups, 2. juveniles, 3. adults, 4. pups and juveniles, 5. pups and adults, 6. juveniles and adults, or 7. pups, juveniles and adults.

Definition: an observation consisted of one recording for each variable.

Generated variables.

These variables were calculated from the original observations and were designed to provide a more-complete picture of the environmental conditions and biotic activities of the seals at the study site.

Group span angle. This variable was formulated as the difference between the group span maximum angle and the group span minimum angle in degrees of magnetic North.

Occupied group distance. From the group span angle, knowing the distance between the seal group on the periphery of a sand bank and the major observation site A, the curvilinear distance in meters along a sand bank shore that a group occupied was calculated. This was accomplished by procedures described by Button (in preparation).

Group density. This variable was calculated using the original data of group number and the generated variable occupied group distance. Group density was the measure of gregariousness and was defined by the formula;

$$\text{group density} = \frac{\text{group number}}{\text{occupied group distance}}$$

In this study, the density of animals used the curvilinear periphery of a seal occupied sand bank as an extreme boundary of inhabited territory. The area necessary to obtain density was the space between the radians of East and West end points of one meter of the sand bank boundary. Thus, a density of 5 seals/meter would numerically describe 5 animals viewed one behind the other in a one meter arc segment.

Haulout rate. The rate of haulout or emergence of seals onto the sand banks was calculated by obtaining the difference in total group numbers for any two successive observations and dividing that figure by the time difference in minutes between the same two observations, i.e.

$$\text{haulout rate} = \frac{\text{group number, obs. 2} - \text{group number, obs. 1}}{\text{hour of obs. 2} - \text{hour of obs. 1}}$$

Tide rate. This variable described the rate of tidal rise or fall and was calculated by dividing the difference in tide height for two successive observations by the time difference between the same two observations, i.e.

$$\text{tide rate} = \frac{\text{tide height, obs. 2} - \text{tide height, obs. 1}}{\text{hour of obs. 2} - \text{hour of obs. 1}}$$

Disturbance. In addition, any interference in the normal pattern of seal haulouts involving a flight reaction in the seal herd was recorded, and the source of the disturbance and its effect noted.

Results

During the study period, 3883 hourly observations of seal groups were made over 157 days.

The data will be presented as follows: first, the descriptive statistics for all variables will be presented, then the correlational relationships for all variables and finally the regression analysis of the behavioural variables.

The means and standard deviations of all variables for the entire study period are presented in Table 4, and for 1971 and 1972 in Table 5.

Air temperature. The maximum air temperature recorded in 1971 was 27.5°C. and 23.0°C. in 1972. The minima were 6°C. in 1971 and -3°C. in 1972. Observers were at the study site on May 30, 1971 and on May 1, 1972, thus colder temperatures were experienced in 1972. The mean air temperature for the entire study period was 14.9°C. with a standard deviation of .078. For the same reason as stated above, the mean air temperature for 1971 ($\bar{X}$ = 16.8, S.D. = 4.88) was higher than that for 1972 ($\bar{X}$ = 13.5, S.D. = 4.38). The mean daily air temperature for the entire study period is presented in Fig. 5. Air temperature was more variable in 1971 than in 1972, probably because the study site attendance by the author was more continuous in the latter year. The very high mean recorded on Day 27 (1971) included only one observation taken at the warmest

Table 4

Means and Standard Deviations of All Variables for the Entire Study Period.

Variable	Mean	Standard Deviation
1. Air temperature (in degrees Centigrade)	14.9 ± 0.1	.078
2. Sea temperature (in degrees Centigrade)	11.5 ± 0.1	5.922
3. Wind speed minimum (in km.p.h.)	12.5	8.194
4. Wind speed maximum (in km.p.h.)	18.2	11.318
5. Cloud cover (in per cent)	.636	.398
6. Tide height (in meters)	1.18	.391
7. Group span minimum (in radians)	1.117	.280
8. Group span maximum (in radians)	1.155	.283
9. Group number	42.24	58.045
10. Haulout rate (in # seals/hour)	8.048	65.478
11. Tide rate (in cm./hour)	-.40	20.900
12. Occupied distance (in meters)	25.3	33.422
13. Group density (in # seals/meter)	1.22	1.067

Table 5

Means and Standard Deviations for All Variables for 1971 and 1972

Variable	1971		1972	
	Mean	S.D.	Mean	S.D.
1. Air temperature	16.8 ± 0.1	4.88	13.5 ± 0.1	4.38
2. Sea temperature	11.2 ± 0.1	7.68	11.8 ± 0.1	4.26
3. Wind speed minimum	11.93	7.64	12.79	8.48
4. Wind speed maximum	17.03	10.36	18.91	11.87
5. Cloud cover	.65	.41	.63	.39
6. Tide height	1.19	.39	1.18	.40
7. Group span minimum	1.15	.23	1.09	.31
8. Group span maximum	1.19	.23	1.13	.31
9. Group number	35.36	51.41	47.08	61.86
10. Haulout rate	13.28	70.31	4.30	60.98
11. Tide rate	-.92	20.43	-.31	20.50
12. Occupied distance	22.07	28.90	27.26	33.61
13. Group density	1.43	.95	1.46	.82

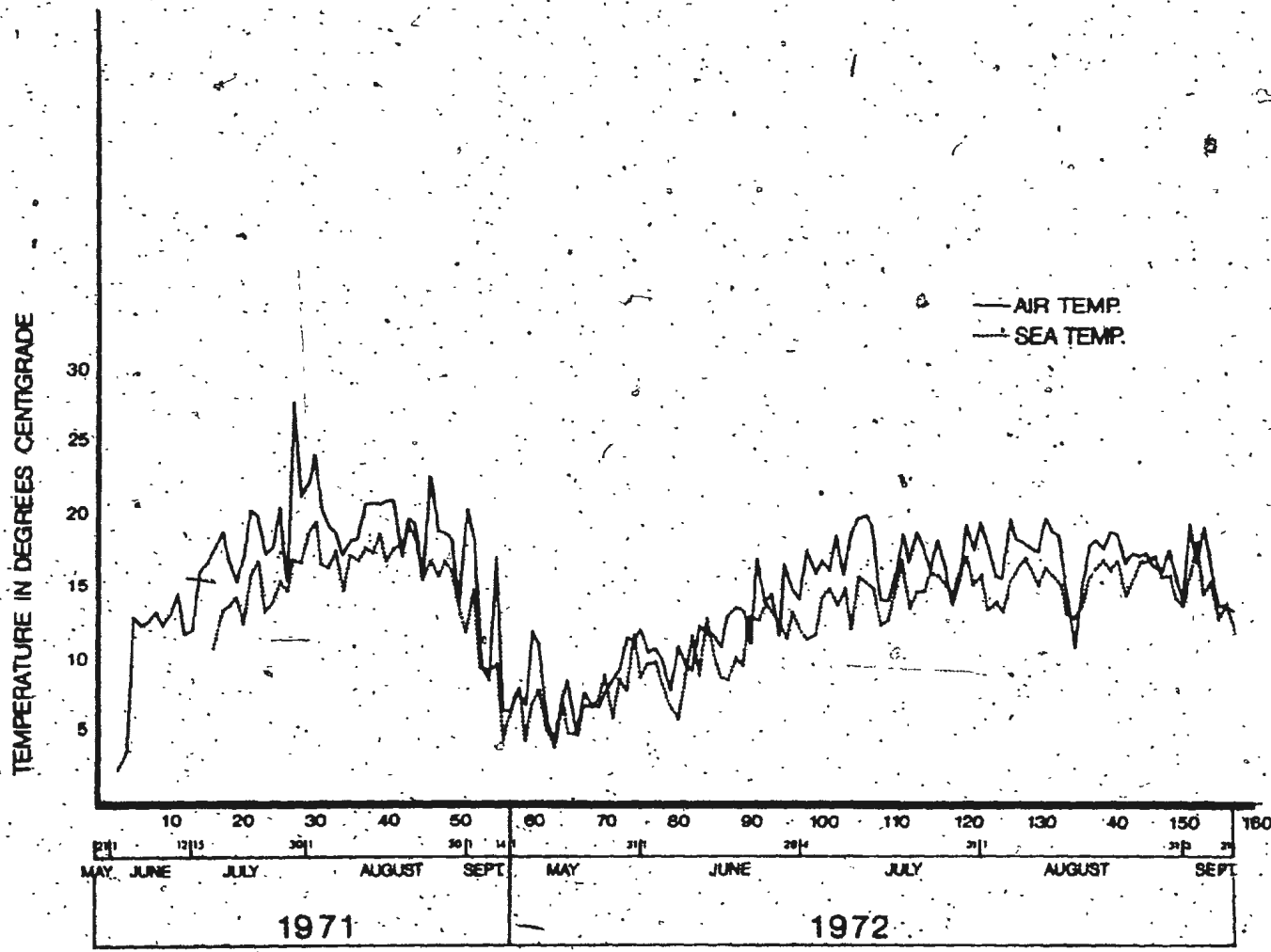

Fig. 5 Mean Daily Air and Sea Temperature at the Study Site

hour of the day

Sea temperature. Sea temperatures in the Grand Barachois were not as extreme as air temperatures. The maximum sea temperature for 1971 was 21°C. and for 1972 was 21.7°C., the highest sea temperature recorded. Barachois waters, due to their shallow depth, warmed greatly during the period between a rising tide and the next low tide, especially on clear days. Oceanic waters outside the Grand Barachois varied from 2°C. in early May to 16.2°C. in mid August.

The mean daily sea temperature, as illustrated in Fig. 5, closely parallels rising and falling air temperatures. The mean sea temperature for the barachois during the seven month study period was 11.5°C.(S.D. = 5.922). The mean sea temperature for 1971 ($\bar{X}$ = 11.21, S.D. = 7.68) closely approximates that for 1972 ($\bar{X}$ = 11.8, S.D. = 4.26). Both sea and air temperatures follow the same patterns of increase through mid summer and decline in the fall. The graph for 1971 is more horizontally compressed since the number of days at the study site was not as great in that year as in 1972. Nevertheless, both years exhibit the same trend of mid July peaks and declines after August 31.

Wind speed minimum. The highest minimum wind speed was 43 km.p.h. on a day when the maximum wind speed was 68 km.p.h. in 1972. The minimum wind speed naturally was zero although this occurred very rarely. The highest

wind speed minimum in 1971 was 42 km.p.h. Mean wind speed minimum for the entire study period was 12.44 km.p.h. S.D. = 8.194). The high standard deviation indicates the fluctuation that was typical of this variable. Mean wind speed minimum for 1971 ($\bar{X}$ = 11.93, S.D. = 7.64) was very similar to that for 1972 ($\bar{X}$ = 12.79, S.D. = 8.48). The mean daily wind speed minimum is presented in Fig. 6.

Wind speed maximum. The highest wind speed maximum was 68 km.p.h. in 1972. In 1971, the highest maximum wind speed was 52 km.p.h. The mean wind speed maximum for the entire study period was 18.177 (S.D. = 11.318). In 1971, the mean wind speed maximum was 17.03 (S.D. = 10.36) while in 1972, the mean wind speed maximum was 18.91 (S.D. = 11.87). As with daily mean wind speed minimum, daily wind speed maxima showed considerable variability from day to day (See Fig. 6). Typically, the wind speed increased daily from 0900 hours to 1630 hours and then subsided. Winds from the North and West were most adherent to this pattern, whereas southerly or easterly winds tended to persist throughout the evening. Southerly winds often brought fog conditions to the Grand Barachois, and breezes from this direction were the most frequent. Some reduction in daily mean wind speed maxima can be seen in Fig. 6 during the periods from mid July to mid August of both study years.

Cloud cover. The mean cloud cover for 1971 was .646 (S.D. = .41) and for 1972 was .629 (S.D. = .39).

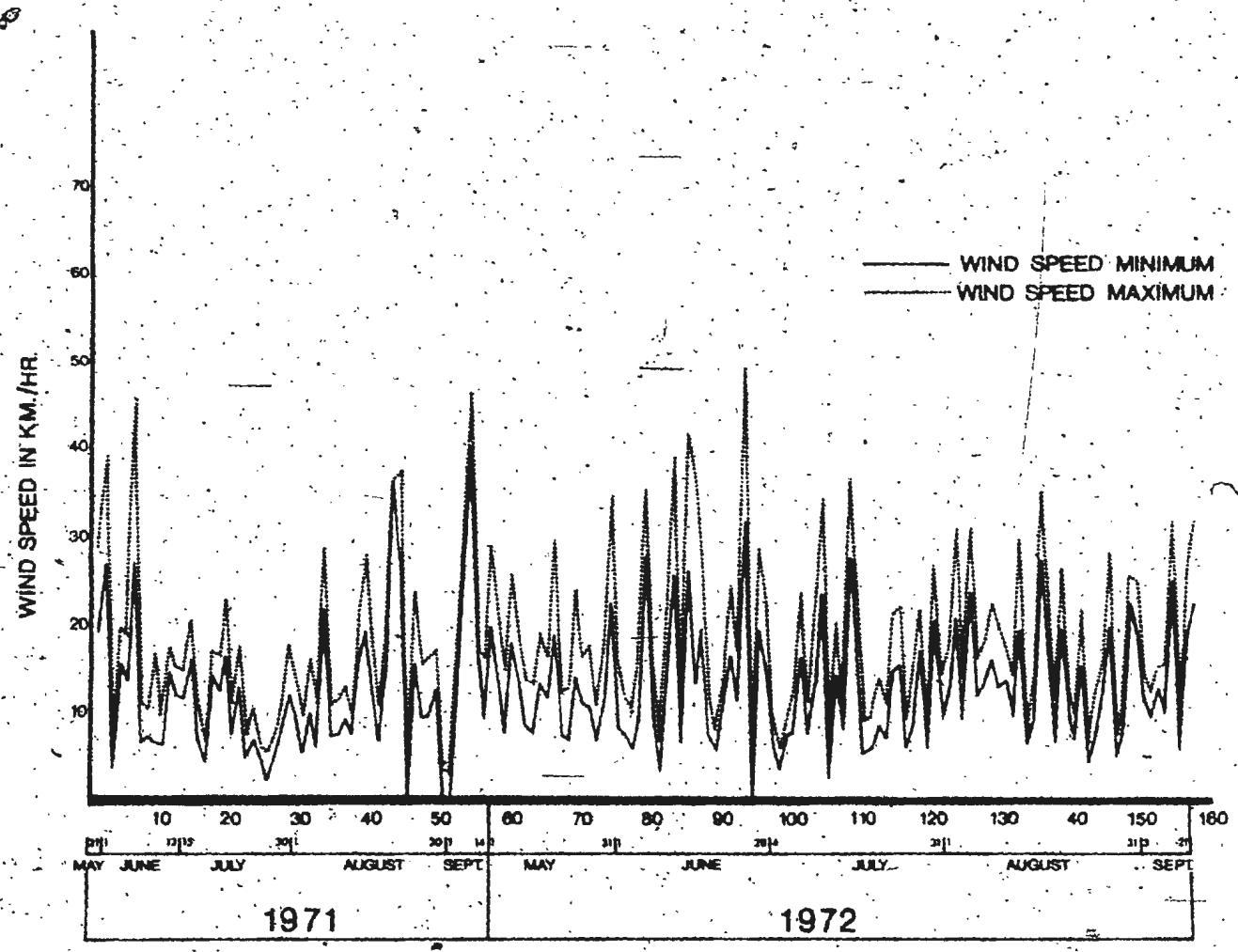

Fig. 6 Mean Daily Wind Speed Minimum and Maximum at the Study Site

These figures indicate the rather typical fog and overcast conditions that dominate the Grand Barachois. No difference appears in yearly amounts of cloud cover. The mean cloud cover for the entire study period was .636 (S.D. = .398). Maxima and minima for both years were one and zero respectively. Great variation in the mean daily cloud cover can be seen in Fig. 7. The low lying geography of the barachois seemed to collect fog whenever it was present in the North Atlantic. Indeed, records show fog occurring for 35 consecutive days in June and early July, 1972, although only dense fog conditions at sea level prevented observations of the seals. Fog at the study site tended to reduce the daily ambient air temperature fluctuations common with clear skies by filtering radiant heat from the sun during the day, performing a heat canopy function to retain day warmth close to the earth, and preventing nocturnal radiant heat losses to the sky.

Tide height. The highest tide experienced at the barachois during the study period was 2.41 m. in 1972 and 2.35 m. in 1971 above chart datum. Tides of greater height than these were present at the study site, however, all sand banks were then submerged leaving no base site for the seal aggregation. Lowest low tide for 1971 was .37 m. and for 1972 was .03 m. Mean tide height for the study period was 1.187 m. (S.D. = .391) above chart datum. Mean tide height for 1971 ($\bar{X}$ = 1.19, S.D. = .39) was almost

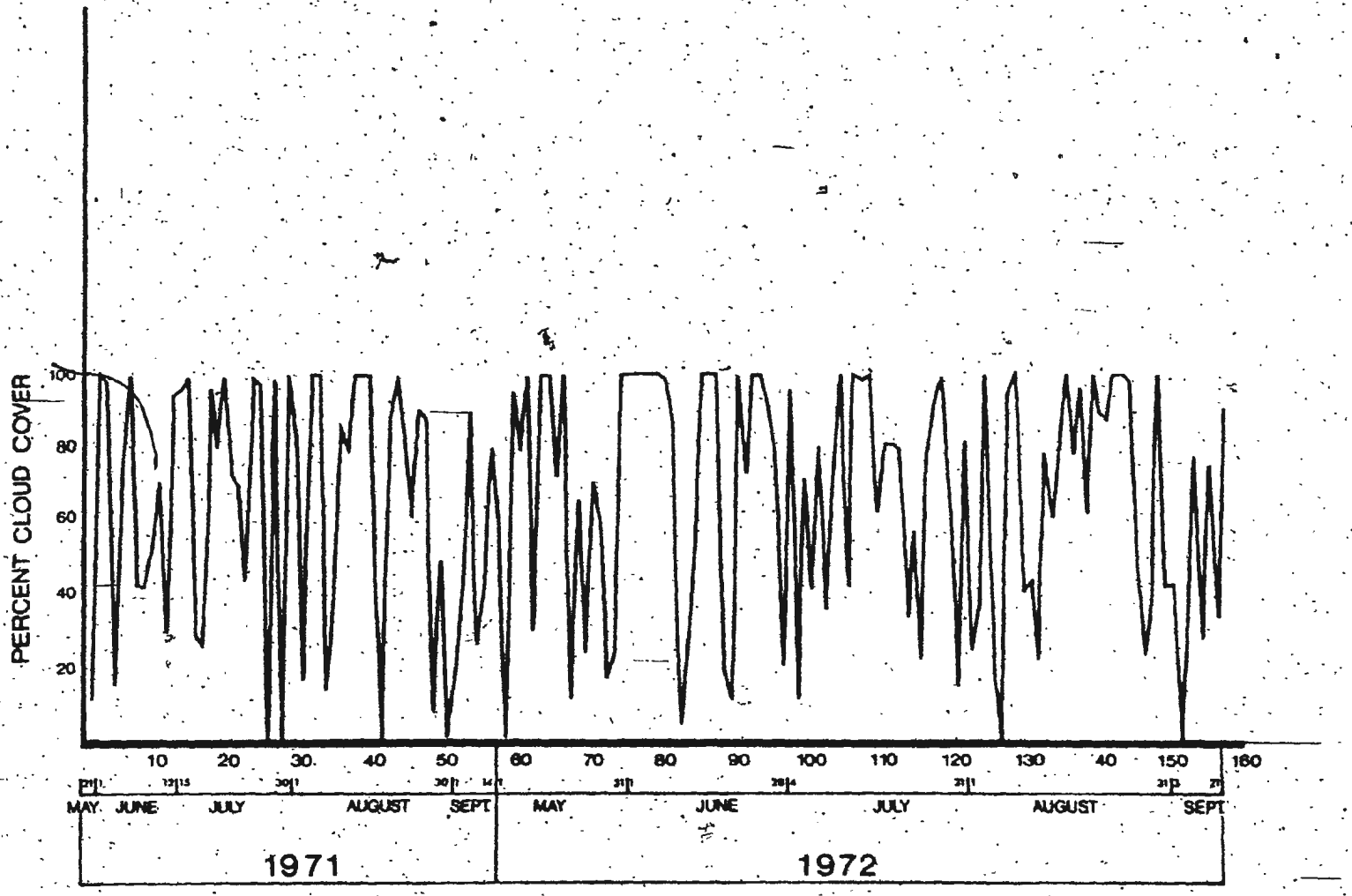

Fig. 7 Mean Daily Cloud Cover at the Study Site

identical to that for 1972 ($\bar{X}$ = 1.18, S.D. = .40). Tidal height changes of one-third of a meter made very significant differences in the amount of sand bank exposure, however, this factor could not be measured consistently with facility.

Tide status. Since tide status was a categorical measure, means and standard deviations would not be meaningful. The relation of tide status to other variables will be discussed with the correlational data.

Tide rate. Rising tide rates of the greatest magnitude during an observation occurred on day 9 (in 1971, 73.2 cm./hr.) and on day 118 (in 1972, 91.5 cm./hr., See Fig. 8). Falling tide rates reached maxima of -51.8 cm./hr. in 1971 and -91.5 cm./hr. in 1972. Although other tide rates during spring tides may have exceeded those reported, the above figures are valid as rates of tide change before an observation sequence. The mean tide rate, thus obtained, for 1971 and 1972 combined was -0.40 cm./hr. (S.D. = 20.9). The mean tide rate for 1971 ($\bar{X}$ = -0.92, S.D. = 20.43) was similar to that for 1972 ($\bar{X}$ = -0.31, S.D. = 20.50). These small means indicate that seal observations were performed equally during decreasing and increasing tides. Hence no bias in the time of observation seems present.

Group span minimum angle. The mean westernmost angle (Magnetic North) for seal groups on the sand banks of the Grand Barachois for the entire study period was 1.117

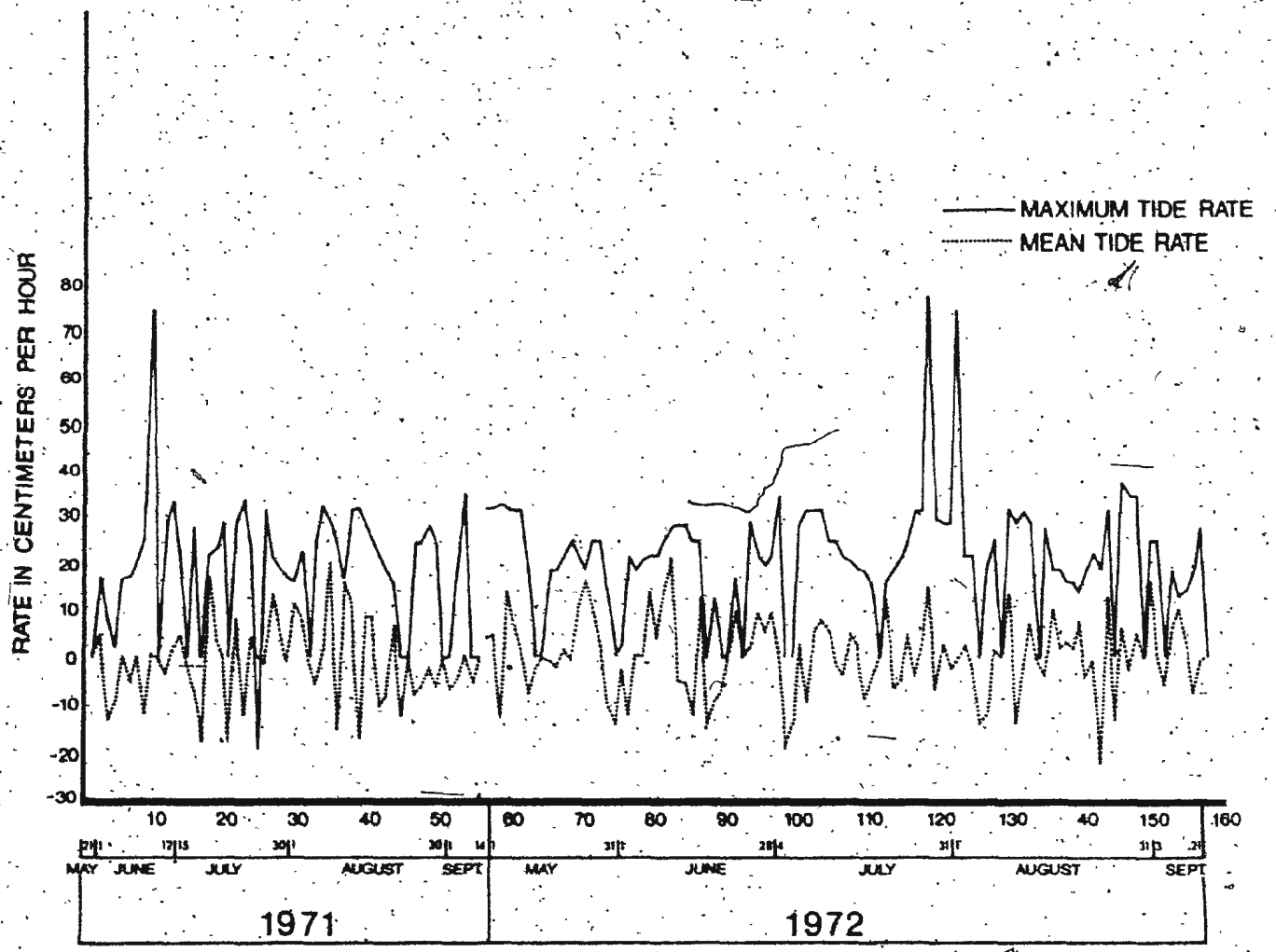

Fig. 8 Daily Mean and Maximum Tide Rate at the Study Site

radians (or 64°), S.D. = .280. The mean westernmost angle of seal groupings in 1971 ($\bar{X}$ = 1.15, S.D. = .23) (65° 50') closely approximated that of 1972 ($\bar{X}$ = 1.09, S.D. = .31) (62° 30'). The mean daily group span minimum angle is presented in Fig. 9.

Group span maximum angle. The mean easternmost angle of seal groupings for the entire study period was 1.155 radians (66° 10' Magnetic), S.D. = .283. The mean group span maximum angle for 1971 ($\bar{X}$ = 1.19, S.D. = .23, 68° 10') was .06 radians greater than that of 1972 ($\bar{X}$ = 1.13, S.D. = .23, 64° 10'). The group span minimum angle also followed this trend by the same radian increment, a difference of 3° 26'. This difference is probably an artifact of the difference in the length of the study period between years 1971 and 1972, the latter providing a more continuous observation period. There were no detectable changes in the position of the major sand banks to account for the yearly differences in mean aggregation position. As can be seen in Fig. 9, there are three noticeable fluctuations in the generally smooth curves of mean daily group span maximum and minimum. On day 50, a disturbance of the seal group at the easternmost end of the sand bank perimeter stampeded the animals to the water and they emerged farther West on the same sand bank. Days 66-73 comprised a week when some disturbance was caused by the observers near observation station B. This had the same

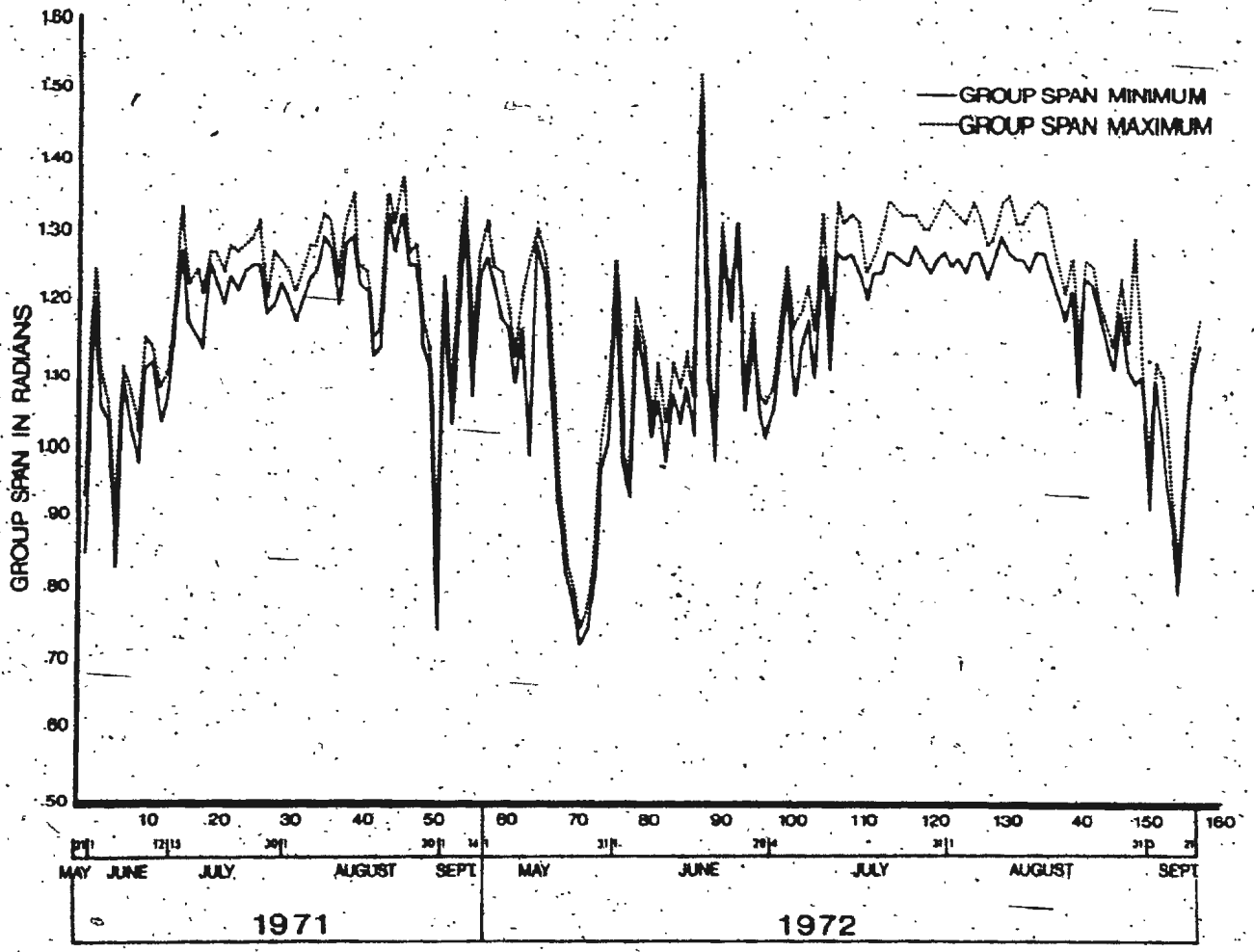

Fig. 9 Mean Daily Group Span Minimum and Maximum of Observed Seal Groups

effect on Day 50 over a longer time period. Day 87 was the only time that seals were observed hauled out on a sand bank at the South side of la Goulet de Langlade, hence the mean group span is inflated. For both years, mid July was the time that seal groupings tended to move eastward on the sand bank periphery.

Group number. The largest discrete group of seals observed during the 1971 study period was 384 animals on day 21, while the largest grouping for 1972 contained 304 seals on day 124. The mean group size for the study was 42.240 animals (S.D. = 58.045). Mean group size for the year 1971 ($\bar{X}$ = 35.36, S.D. = 58.045) was lower than the mean group size for the year 1972 ($\bar{X}$ = 47.08, S.D. = 61.86). Again, this difference is probably due to observation attendance at the study site in 1971 being during periods of low aggregation size. The 1972 figure then would probably be more valid. In both years, increases in daily maximum number of seals in observed seal groups commenced in early June and decreased again in mid August (see Fig. 10). The daily mean number of seals in observed groups reflects this trend.

Group occupied distance. The largest linear distance along a sand bank occupied by a seal group was 171 m. in 1971 and 173 m. in 1972. The mean curvilinear distance that seal groups occupied was 25.319 m. for the entire study period. The mean occupied distance for seal groups

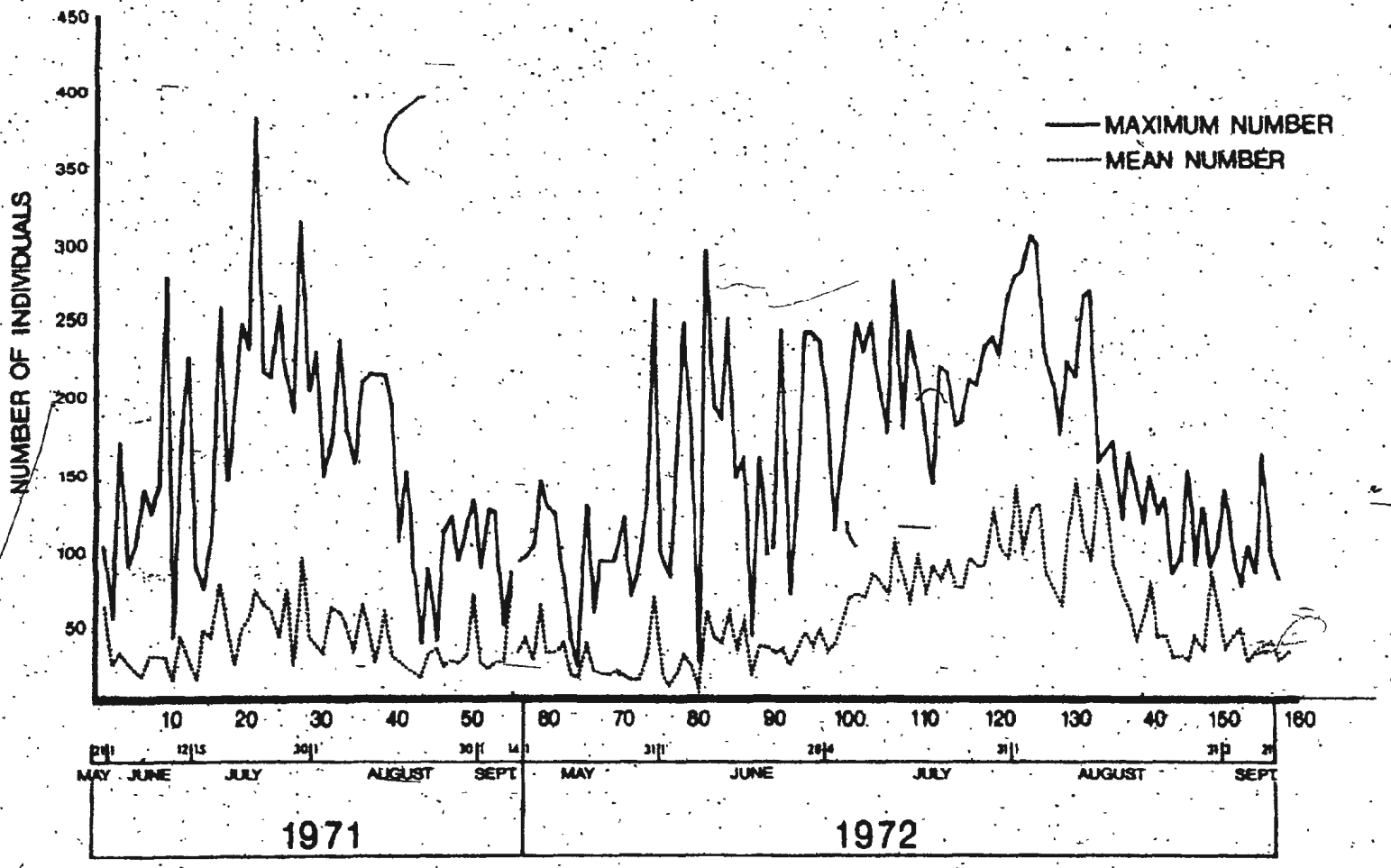

Fig. 10 Daily Mean and Maximum Number of Seals in Observed Seal Groups

in 1971 was 22.07 m. (S.D. = 28.9) but was somewhat greater for 1972 ($\bar{X}$ = 27.26, S.D. = 33.61). This increase was probably due to the increased group size in 1972 over the previous year.

Haulout rate. The maximum haulout rate for 1972 was 388 seals/hour. This figure represents 194 seals hauling out within one-half hour. The most rapid aquatic immersion of a seal group in 1972 was 401 seals/hour. The maximum haulout rate for 1971 was 312 seals/hour and the maximum immersion rate was 882 seals/hour. The latter figure represents a group of 220 seals stampeding into the water over a 15 min. period.

The mean haulout rate for the entire study period was 8.048 seals/hour (S.D. = 65.478). The mean haulout rates for 1971 and 1972 independently were $\bar{X}$ = 13.28, S.D. = 70.31; $\bar{X}$ = 4.30, S.D. = 60.98 respectively. These were the only means of all variables studied that showed a great difference annually. Since haulout rate is a composite of the rate of emergence (a positive number) and the rate of re-entry (a negative number) to the water, haulout rate was divided thus and analysed for each year and species. Emergence and re-entry rates were found to be identical to the overall haulout rates for each species and year (See Tables 5 and 6).

Haulout rates, or emergence and re-entry rates, changed for each species from 1971 to 1972. The mean haulout

Table 6

Means and Standard Deviations of Behavioural Measures of Observed Seal Groups of *Phoca vitulina* and *Halichoerus grypus*.

Variable	*Phoca vitulina*		*Halichoerus grypus*	
	Mean	S.D.	Mean	S.D.
1. Group span minimum	1.08	.30	1.24	.13
2. Group span maximum	1.12	.31	1.25	.13
3. Group number	54.11	63.89	11.14	12.78
4. Haulout rate	8.28	67.09	7.72	59.37
5. Occupied distance	31.41	34.99	8.63	9.33
6. Group density	1.54	.90	1.21	.75

rate for P. vitulina in 1971 was 13.96 (S.D. = 74.74) while in 1972 the mean rate decreased to 4.84 (S.D. = 61.77). For H. grypus, as well, the 1971 mean haulout rate ($\bar{X}$ = 12.32, S.D. = 50.51) was much larger than that of the following year ($\bar{X}$ = 2.98, S.D. = 57.86). This difference may be explained by two facts: 1. haulout rate is a reflection of group number over time and group number itself showed some differences from year to year, 2. Some emergence sequences were studied more extensively than aquatic re-entry sequences in 1971. Hence positive haulout rates were not as greatly cancelled out by negative re-entry rates as in 1972 when haulouts and re-entries were equally observed. As can be seen in Fig. 11, there does not appear to be a general pattern of daily mean and maximum haulout rates of seals. Maximum haulout rates are extremely variable and were observed to radically fluctuate according to the time of the observation, the interval between observations, whether the haulout was in initial rapid stages at just decreasing tides or well formed at near low tide.

Group density. The maximum group density observed was 15.023 seals/meter in 1971 and 11.438 seals/meter in 1972. The mean group density for the entire study period was 1.223 seals/meter, S.D. = 1.067). There was very little difference between the mean group densities for 1971 and 1972 ($\bar{X}$ = 1.43, S.D. = .95; $\bar{X}$ = 1.46, S.D. = .82

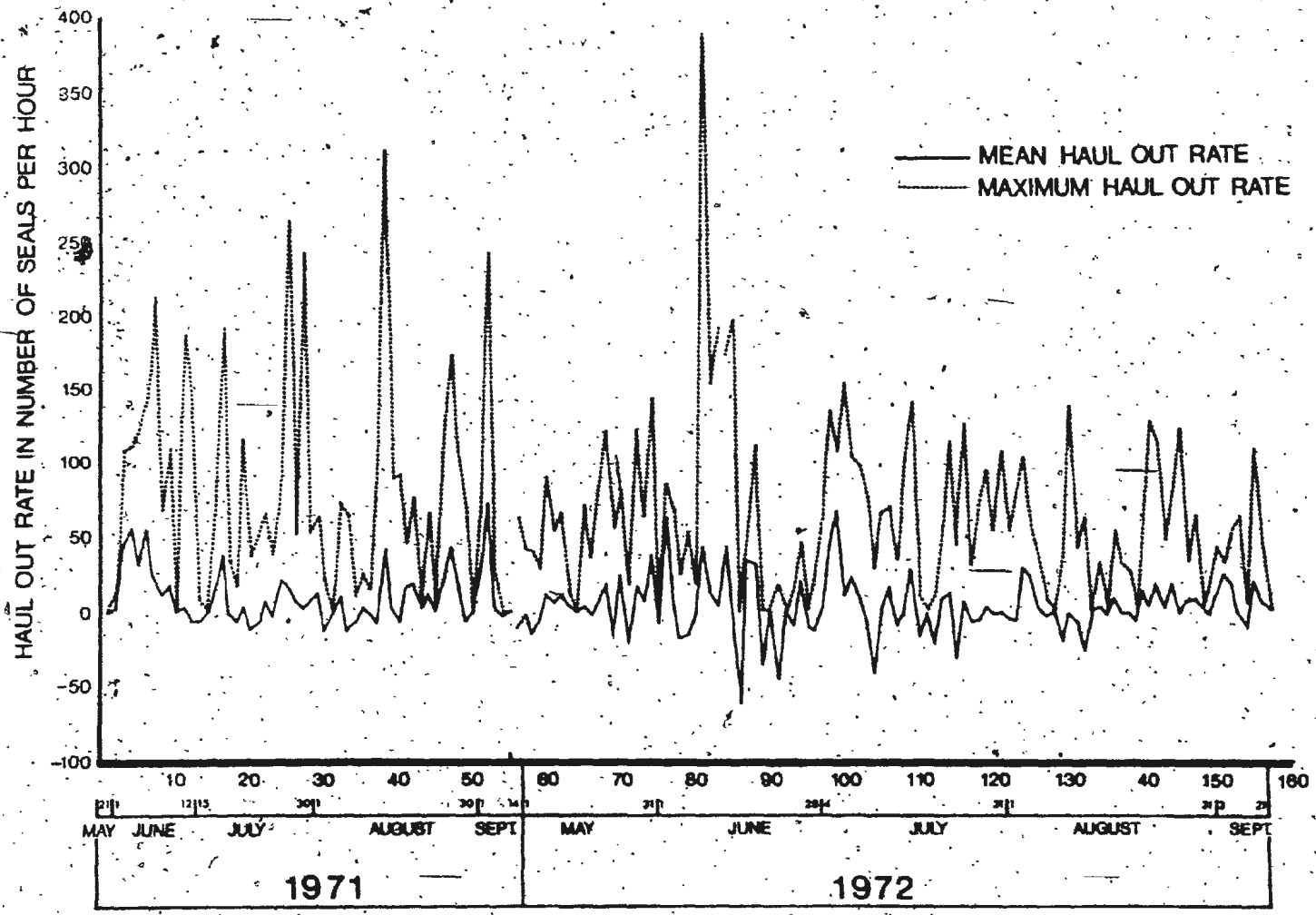

Fig. 11 Daily Mean and Maximum Haulout Rate of Observed Seal Groups

respectively). Group density increased from June 1 to a peak on August 14 and thereafter decreased rapidly in 1972. No similar pattern appears from the data for 1971, probably as a result of fewer observations in August of that year (See Fig. 12).

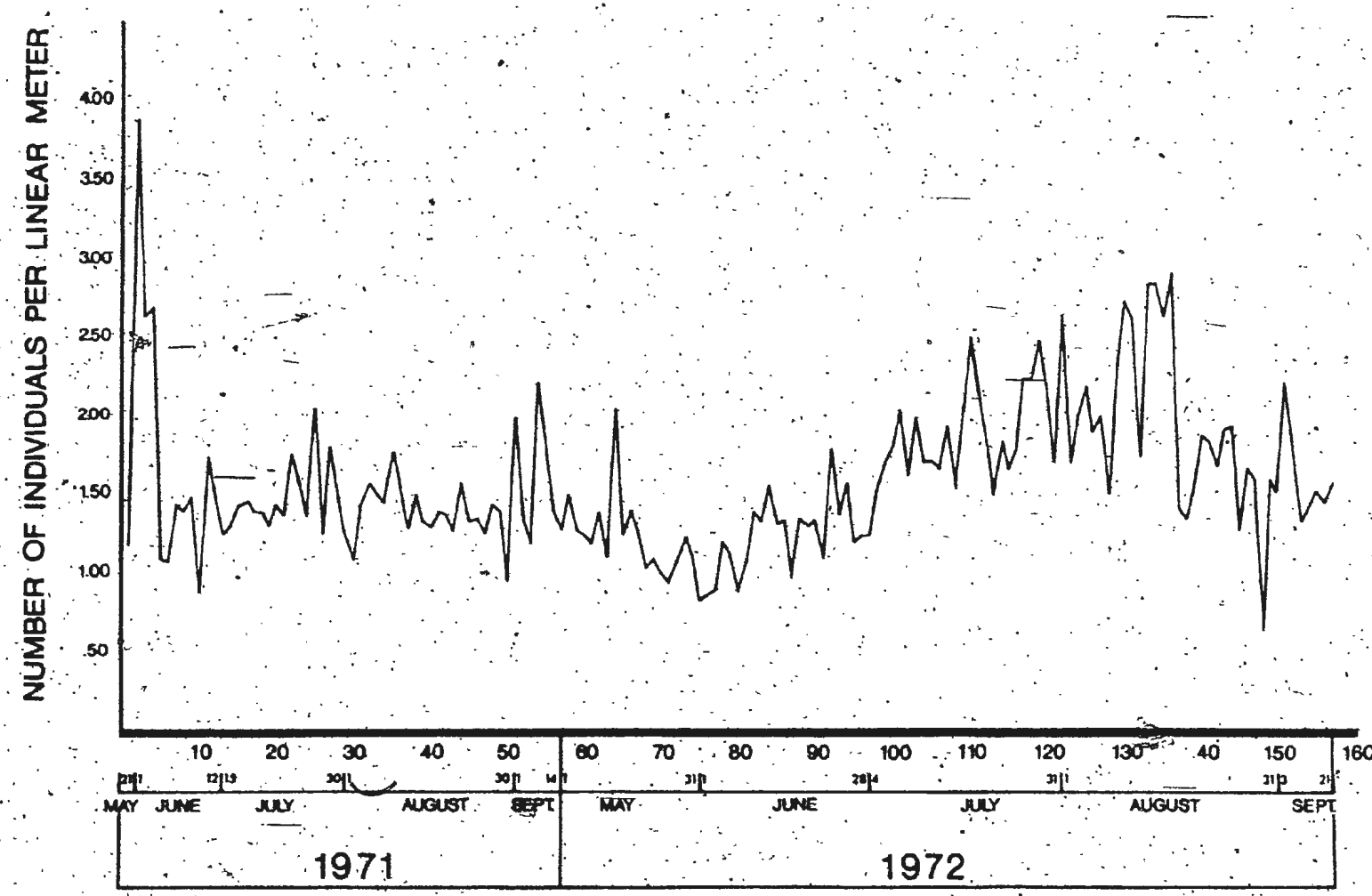

Fig. 12 Mean Daily Group Density of Observed Seal Groups

Species differences on behavioural variables.

The previous data on behavioural measures were for Phoca vitulina and Halichoerus grypus. These measures were also analysed specifically. Means and standard deviations of all behavioural variables according to species are presented (Table 6).

Group span minimum and maximum angle. The means of both group span minimum and maximum were smaller for the Harbour Seal ($\bar{X}$ = 1.08 (61°50'), S.D. = .30; $\bar{X}$ = 1.12 (64°10'), S.D. = .31 respectively) than for the Grey Seal ($\bar{X}$ = 1.24 (71°10'), S.D. = .13; $\bar{X}$ = 1.25 (71°40'), S.D. = .13 respectively), indicating a wider group span for the Harbour Seal and a smaller group span, as well as a typically more easterly location on the sand banks, for the Grey Seal.

Group number. The Harbour Seal exhibited a much larger mean group size ($\bar{X}$ = 54.11, S.D. = 63.89) than the Grey Seal ($\bar{X}$ = 11.14, S.D. = 12.78). Maximum group size followed the same trend, the maximum group size of the Harbour Seal was 382, for the Grey Seal only 68. The daily mean number of seals in groups of the Harbour Seal and the Grey Seal is presented in Fig. 13. The daily mean number of P. vitulina closely approximates that for both species combined (See Figs. 10 & 13). This parallel probably occurs because the fluctuations in

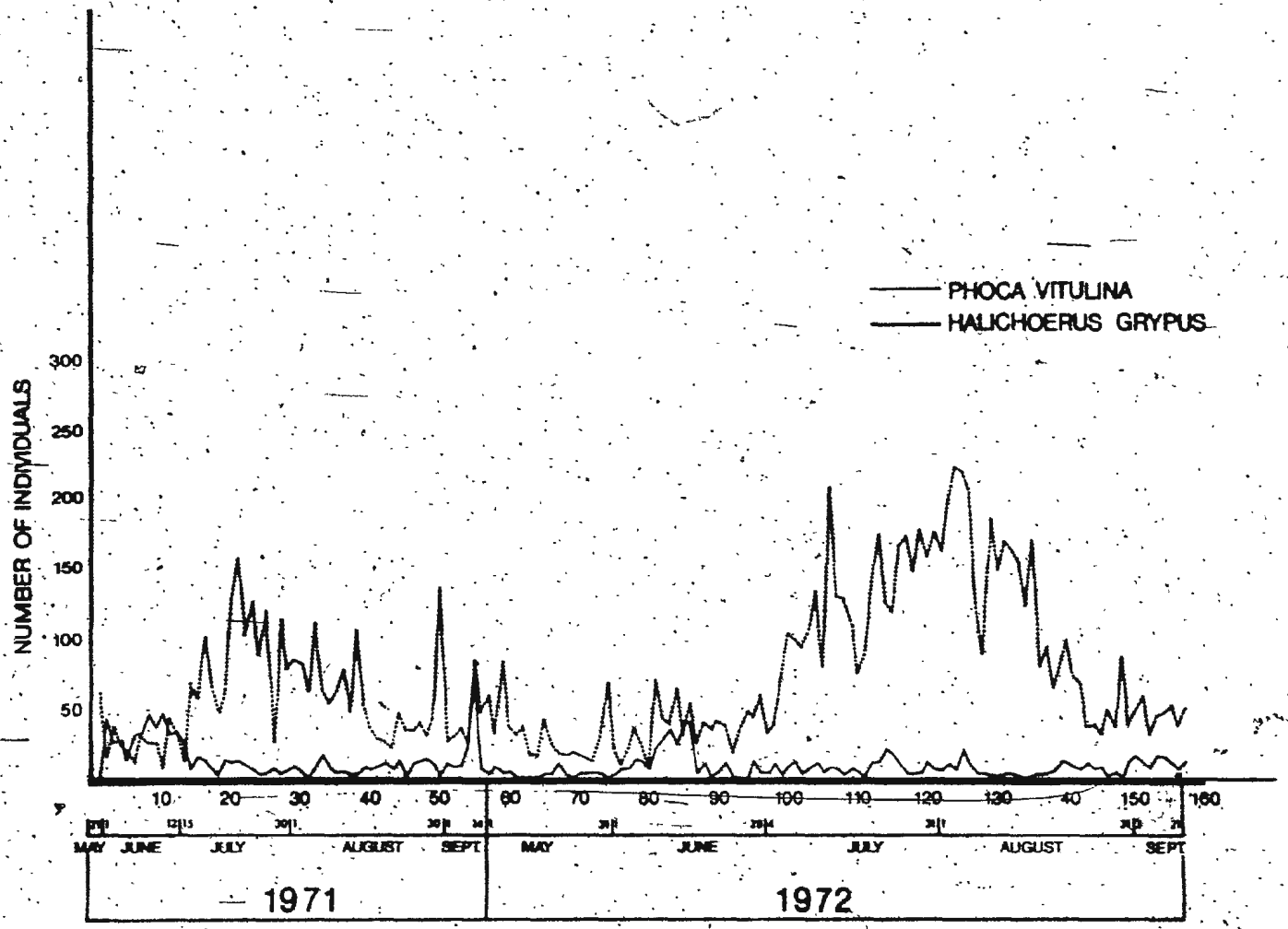

Fig. 13 Daily Mean Number of Seals in Groups Comprised of Phoca vitulina and Halichoerus grypus

group number of P. vitulina were much greater than those of H. grypus, and the former species comprised a much greater number than did the latter species. The Grey Seal showed increased terrestrial preference during early June of both 1971 and 1972 (Fig. 13, days 2-12 and 80-86).

Haulout rate. There was not a great difference in haulout rates of the two species of seals (P. vitulina, $\bar{X}$ = 8.28, S.D. = 67.09; H. grypus, $\bar{X}$ = 7.72, S.D. = 59.37) over the entire study period. However, the author did observe behavioural differences between the two species in the pattern of haulout. The Harbour Seal exhibited a rather casual method of haulout. Haulout usually commenced with one or two juveniles who ventured onto the sand banks and returned to the water several times thereafter. As soon as one animal emerged, it was followed by 5-15 others which had been watching this procedure. Numbers then increased to a maximum prior to low tide. Grey Seals tended to haulout in force. During the study period, 10-20 animals were observed to approach and emerge onto the sand banks in a rapid sequence. This haulout occurred usually at ½ to 1/3 falling tide, after a substantial group of Harbour Seals had already emerged.

Occupied group distance. Mean occupied distance in linear meters along a sand bank was smaller in H. grypus ($\bar{X}$ = 8.63, S.D. = 9.33) than in P. vitulina ($\bar{X}$ = 31.41, S.D. = 34.99). This varied concommittantly with and was

probably a result of the differences in group number in the two species (See Table 6).

Group density. Groups of P. vitulina were commonly more compact ($\bar{X}$ = 1.54 seals/meter, S.D. = .90) than groups of H. grypus ($\bar{X}$ = 1.21 seals/meter, S.D. = .75). This was probably due to the greater size of the individuals of the latter species (See Table 2) rather than an increased distance between animals.

Frequencies of observations of species, sex, haulout location and age of seal groups.

Species. Of the 3883 aggregations of seals sighted at the Grand Barachois over the entire study period, 2812 (72.4%) were groups of P. vitulina exclusively, 1063 (27.4%) were groups of H. grypus, and one group, under disturbed conditions, contained both species (See Table 7). Seven groups (0.02%) could not be classified according to species because of poor visibility. In 1971, 1060 (66.2%) of the 1601 seal groups sighted contained P. vitulina and only 538 (33.6%) contained H. grypus (See Table 8). Three groups (0.02%) were unclassified during that year. The following year's frequency distribution was similar, although there were 2281 seal groups observed in 1972. The greater proportion of groups again contained P. vitulina. Some 1752 groups (76.8%) were composed of this species and 525 (23.0%) were composed of H. grypus. Four groups (0.02%) were unclassified according to species for 1972, (Table 8).

Sex. The breakdown of groups into sex classes showed that females of both species combined formed groups more frequently than males (See Table 7). Of the 3883 sightings, however, the greatest proportion (2679 or 68.9%) of groups was composed of both sexes, 611 (15.7%) groups contained exclusively females and 299 (7.9%) groups contained only males. Due to poor visibility and other

Table 7

Absolute and Relative Frequencies of Observed Seal Groups According to Species, Sex and Haulout Location Categories for the Entire Study Period.

Variable	Categories				
Species	*Phoca vitulina*	*Halichoerus grypus*	Both Species	Unknown	
Absolute frequency	2812	1063	1	7	
Relative frequency (per cent)	71.4	27.4	0.0	0.2	
Sex	Male	Female	Both Sexes	Unknown	
Absolute frequency	299	611	2679	294	
Relative frequency (per cent)	7.9	15.7	68.9	7.6	
Haulout location	Station 0	Station 1	Station 2	Station 3	Station 4*
Absolute frequency	3669	164	33	14	3
Relative frequency (per cent)	94.5	4.2	0.8	0.4	0.1

*See Figure 2 for Station locations.

Table 8

Absolute and Relative Frequencies of Observed Seal Groups According to Species, for 1971 and 1972.

		Species Categories			
		Phoca vitulina	Halichoerus grypus	Both Species	Unknown
Absolute frequency	1971	1060	538	0	3
	1972	1752	525	1	4
Relative frequency (per cent)	1971	66.2	33.6	0	0.2
	1972	76.8	23.0	0	0.2

difficulties, 294 (7.6%) groups could not be classified according to sex. The mean daily frequencies of seals in groups of males, females, or both sexes are presented (Fig. 14). Female groups predominate in late May and early to mid June, which is the period of pupping and suckling in P. vitulina. Male groups also increase during this time, associated with female deletion.

Annual differences in the number of male and female groups were not great (See Table 9). In 1971, 140 (8.7%) groups were exclusively male and the next year, 159 (7.0%) groups were all male. Female groups numbered 239 (14.9%) of the 1601 groups in 1971 and 372 (16.3%) of the 1972 total of 1752 groups. A large predominance of groups containing both sexes occurred during the study (1971, 1142 or 71.3%; 1972, 1537 or 67.4%). Some 80 groups (5.05%) could not be classified according to sex in 1971 and 214 (9.4%) in 1972.

The majority of P. vitulina groups observed were composed of both sexes (2002 or 71.2%, See Table 10). Female P. vitulina comprised 463 (16.5%) of groups of that species and 65 (2.3%) male groups were observed. Sex unclassified groups of the Harbour Seal accounted for 282 (10%) groups. Of the 1063 groups of H. grypus observed 677 (63.7%) were of both sexes, 234 (22.0%) males and 147 (13.8%) females. Five (.05%) groups were unclassi-

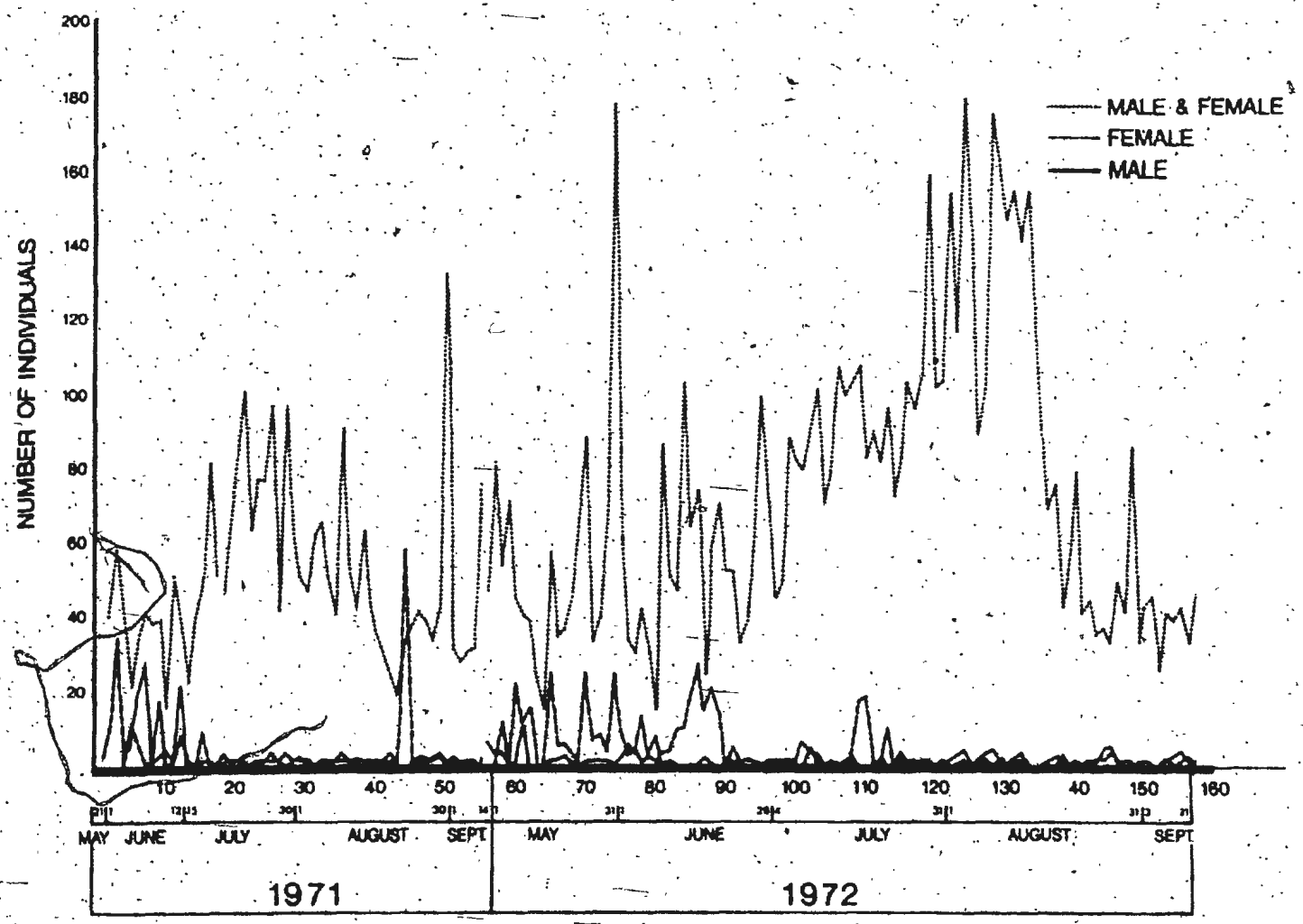

Fig. 14 Daily Mean Number of Seals in Groups Comprised of Males, Females and Both Sexes

Table 9

Absolute and Relative Frequencies of Observed Seal Groups According to Sex, for 1971 and 1972.

		Sex Categories			
		Male	Female	Both Sexes	Unknown
Absolute frequency	1971	140	239	1142	80
	1972	159	372	1537	214
Relative frequency (per cent)	1971	8.7	14.9	71.3	5.0
	1972	7.0	16.3	67.4	9.4

Table 10

Absolute and Relative Frequencies of Observed Seal Groups of *Phoca vitulina* and *Halichoerus grypus* according to Sex.

		Sex Categories			
		Male	Female	Both Sexes	Unknown
Absolute frequency	*P. vitulina*	65	463	2002	282
	H. grypus	234	147	677	5
Relative frequency (per cent)	*P. vitulina*	2.3	16.5	71.2	10.0
	H. grypus	22.0	13.8	63.7	0.5

fied.

Haulout location. Of the five haulout locations in the Grand Barachois, Station 0 was most frequently occupied (See Fig. 2 and Table 7). There were 3669 (94.5%) of a total of 3883 groups observed at that site. The only other frequently used site was Station 1 which was used during the pupping season (164 or 4.2%). Station 2 was inhabited by 33 groups (0.8%), Station 3 had 14 groups (0.4%) and Station 4 had 3 groups (0.1%).

Table 11 illustrates an annual change in the frequency with which normal base sites for the two species of seals were inhabited. In 1971, Station 0 was occupied by 1493 groups (93.3%) while in 1972, it was occupied by 2176 groups (95.4%). The greatest yearly changes were in Station 1, which was occupied more heavily in 1971 (106 groups, 6.6%) than in 1972 (58 groups, 2.5%). Station 2, was occupied less frequently in 1971 (2 groups, 0.1%) than in 1972 (31 groups, 1.4%). Stations 3 and 4 were not utilized in 1971 but in 1972 14 groups (0.6%) occupied Station 3 and 3 groups (0.1%) Station 4.

Both P. vitulina and H. grypus exhibited a strong site tenacity for Station 0 (See Table 12).

Table 11

Absolute and Relative Frequencies of Observed Seal Groups According to Haulout Location for 1971 and 1972

		Haulout Locations				
		Station 0	Station 1	Station 2	Station 3	Station 4*
Absolute frequency	1971	1493	106	2	0	0
	1972	2176	58	31	14	3
Relative frequency (per cent)	1971	93.3	6.6	0.1	0.0	0.0
	1972	95.4	2.5	1.4	0.6	0.1

*See Fig. 2 for Station Descriptions

Table 12

Absolute and Relative Frequencies of Observed Seal Groups of *Phoca vitulina* and *Halichoerus grypus* according to Haulout Location.

		Haulout Locations				
		Station 0	Station 1	Station 2	Station 3	Station 4*
Absolute frequency	*P. vitulina*	2606	157	32	14	3
	H. grypus	1062	0	1	0	0
Relative frequency (per cent)	*P. vitulina*	92.7	5.6	1.1	0.5	0.1
	H. grypus	99.9	0.0	0.1	0.0	0.0

*See Figure 2 for Station descriptions.

P. vitulina groups were observed on Station 0, 2606 times (92.7%) while H. grypus groups were observed there 1062 times (99.9%). Station 1 was used only by P. vitulina dams with young (154 groups, 5.6%). Station 2 was also frequented only by P. vitulina (32 groups, 1.1%), with the exception of one H. grypus female (0.1%) that was observed there for a short time. Stations 3 and 4 were occupied solely and rarely by P. vitulina during the postpartum period (14 sightings, 0.5%; 3 sightings, 0.1% respectively).

Age. Of the total 3883 groups of seals observed, 132 (3.4%) groups were composed of pups, 182 groups (4.7%) were juveniles and 1213 groups (31.2%) were adults (Table 3). Groups composed of combinations of these age classes were observed for 60% of the recorded sightings. Pups and juveniles were observed in 58 groups (1.5%). Adults and pups, a class reserved for postpartur-ient females with their progeny of that year, was observed at 514 recordings (13.2%). All three age classes were observed at 678 recordings (17.5%), adult and juvenile at 1080 sightings (27.8%). Only 26 groups (0.7%) could not be classified according to age.

Table 13

Absolute and Relative Frequencies of Observed Seal Groups According to Age for the Entire Study Period.

Age Category	Absolute Frequency	Relative Frequency (per cent)
1. Pup	132	3.4
2. Juvenile	182	4.7
3. Adult	1213	31.2
4. Pup and Juvenile	58	1.5
5. Adult (female) and Pup	514	13.2
6. Adult and Juvenile	1080	27.8
7. Adult, Juvenile and Pup	678	17.5
8. Unknown	26	0.7

For most age classes, the increase in the frequency of class sightings in 1972 was proportionate to the increase in the total number of group sightings in 1972 over 1971. This is illustrated in Table 14 by the annual relative frequencies of observed age classes. Although the absolute frequency of adult groups increased from 1971 to 1972 (468 ; 745 respectively), the relative frequency was similar for 1971 (29.2%) and 1972 (32.6%). The same trend was evident in the pup and juvenile class (1971, 11 groups, 0.7%; 1972, 47 groups, 2.1%), adult and pup class (1971, 190 groups, 11.9%; 1972, 324 groups, 14.2%), adult and juvenile class (1971, 451 groups, 28.2%; 1972, 629 groups, 27.6%) and the class composed of adults, juveniles and pups (1971, 269 groups, 16.8%; 1972, 409 groups, 17.9%). Of all age classes, groups comprised of adults were the most frequent for both study years. A decrease in the relative frequency of pup groups in 1972 from 1971 (1971, 4.1%; 1972, 2.9%) was due to a less frequent occupation of Station 1 in 1972 by pup groups (See Table 11). The number of juvenile age class groups observed in 1972 (56 groups, 2.5%) was reduced from the previous year (126 groups, 7.9%). This decrease was countered however by the association of juveniles with other age classes to a greater extent in 1972 (i.e. pup & juvenile class, adult and juvenile class, Table 14). Fewer groups were age unclassified in 1972 (6 groups, 0.3%) than in 1971 (20 groups, 1.2%) probably as a result of the author's

Table 14

Absolute and Relative Frequencies of Observed Seal Groups According to Age for 1971 and 1972.

Age Category	Absolute Frequency		Relative Frequency (per cent)	
	1971	1972	1971	1972
1. Pup	66	66	4.1	2.9
2. Juvenile	126	56	7.9	2.5
3. Adult	468	745	29.2	32.6
4. Pup and Juvenile	11	47	0.7	2.1
5. Adult (female) and Pup	190	324	11.9	14.2
6. Adult and Juvenile	451	629	28.2	27.6
7. Adult, Juvenile and Pup	269	409	16.8	17.9
8. Unknown	20	6	1.2	0.3

increased experience in age identification techniques.

Of the 2820 groups of P. vitulina observed during the entire study period, 132 groups (4.7%) were exclusively pups, 105 groups (3.7%) juveniles, and 569 groups (20.2%) adults (Table 15). Pup and juvenile class groups were rare (58 groups, 2.1%). Adult and pup class groups comprised 510 groups (18.1%) adult and juvenile 746 (26.5%). P. vitulina groups composed of adults, juveniles and pups (675, 24%) were less frequent than adult and juvenile class groups since the former occurred only after weaning around June 1 (See Fig. 15).

Since no pups of the species H. grypus were ever observed at the Grand Barachois, no age classes containing pups were ever recorded (Table 15). Of the 1063 Grey Seal groups sighted, 77 (7.2%) contained juveniles, 644 (60.6%) adults and 337 (31.7%) both adults and juveniles. Only 3 groups of H. grypus (0.3%) were not age classified and 17 (0.6%) groups of P. vitulina. This was due to the relative ease of aging H. grypus as compared to P. vitulina, under poor visibility using not only size but cranial conformation (See Table 2).

The sequence of group formation pertaining to parturition and pup nutrition of P. vitulina was similar for 1971 and 1972 (See Fig. 16). The first pups were already

Table 15

Absolute and Relative Frequencies of Observed Seal Groups of *Phoca vitulina* and *Halichoerus grypus* According to Age.

Age Category	Absolute Frequency		Relative Frequency (per cent)	
	P. vitulina	*H. grypus*	*P. vitulina*	*H. grypus*
1. Pup	132	0	4.7	0.0
2. Juvenile	105	77	3.7	7.2
3. Adult	569	644	20.2	60.6
4. Pup and Juvenile	58	0	2.1	0.0
5. Adult (female) and Pup	510	0	18.1	0.0
6. Adult and Juvenile	746	337	26.5	31.7
7. Adult, Juvenile and Pup	675	0	24.0	0.0
8. Unknown	17	3	0.6	0.3

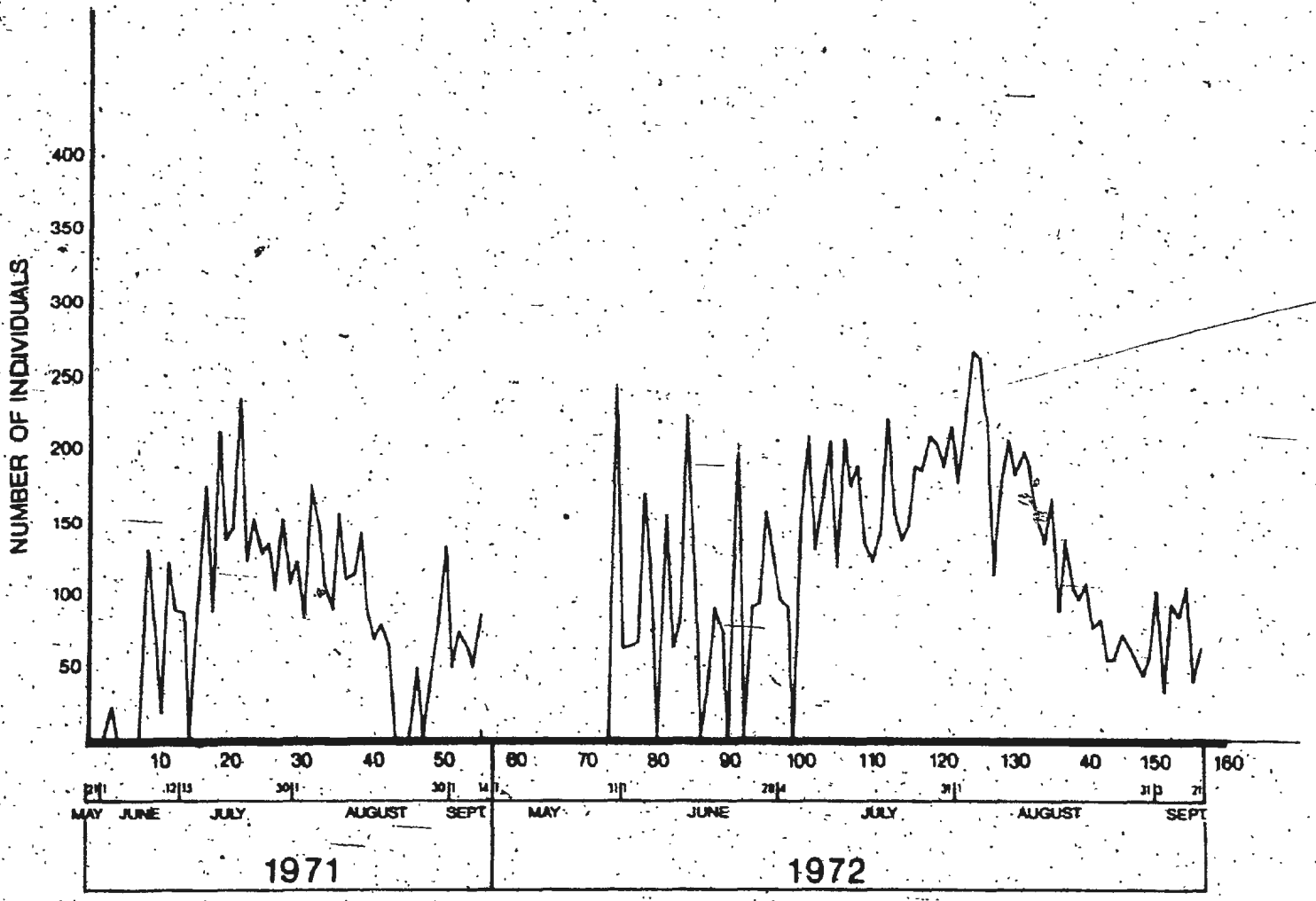

Fig. 15 Daily Mean Number of Seals in Groups Comprised of Pups, Juveniles and Adults

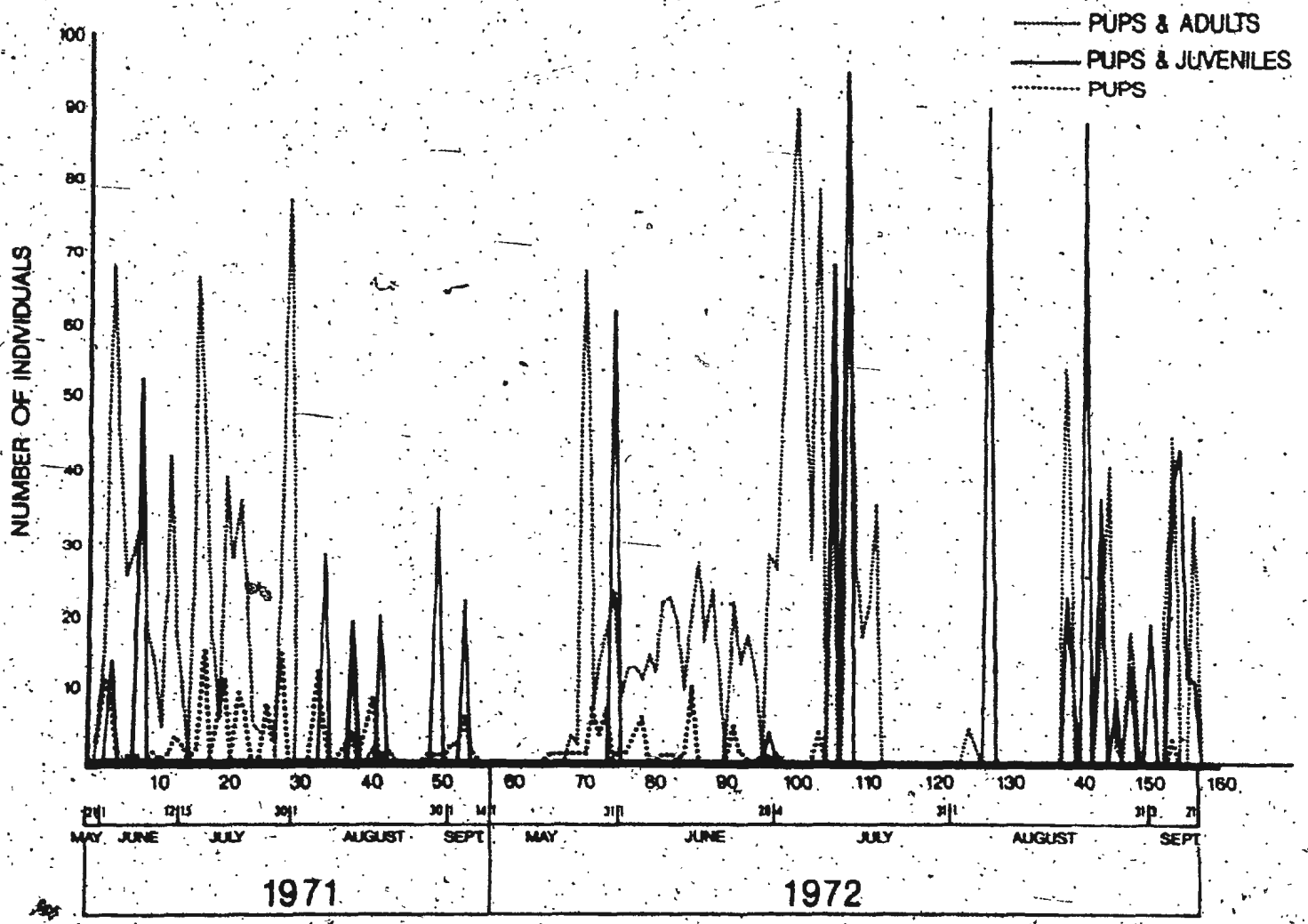

Fig. 16 Daily Mean Number of Seals in Groups Comprised of Pups, Pups and Juveniles, and Pups and Adults

evident when observations commenced on May 30, 1971. A preliminary survey of the study site (Ling & Button, 1973) on May 5, 1970 revealed two P. vitulina pups obviously stillborn and still in lanugo. Premature births were frequently non-viable in 1971 when one stillborn P. vitulina pup was collected and in 1972 when 5 such animals were collected. In 1972, the first pups were noticed on day 65 (May 22). Almost a week thereafter (day 70) a large aggregation of female adults with a few pups formed near the western extremity of Station 0. The same phenomenon occurred on June 1, 1971.

The numbers of P. vitulina pups in discrete groups decreased in 1972 from 1971 concommittant with a relative disuse of the preferred pup haulout site of 1971. Pups were thus more assimilated into other groups of juveniles or adults in 1972 (Figs. 15 & 16). By the end of July in both 1971 and 1972, pups were rarely seen in the presence of adult females only. The peaks on days 7 and 74 (Fig. 16), showing large aggregations of pups and juveniles, were artifacts produced by the human disturbances of the seals on those days, but this combination of age classes was frequently observed from the first week of August of both 1971 and 1972. The peaks of the pup and juvenile class on days 105 and 107 (Fig. 16) are misleading since the groups with one exception were all juveniles. One pup, either orphaned or lost, joined the group on these two days.

The first group of seals comprising pups, juveniles and adults was noticed in the Grand Barachois on June 1, 1971 and on May 30, 1972 (Fig. 15). Although the number fluctuated, a relatively high daily mean number of seals in this age class group was maintained until the middle of August in both years (days 40 and 136, Fig. 15). The groups then decreased in number until the end of August when mean numbers again increased. Strong similarities in the variability of daily means for the month of June to the consistently high numbers for the following 45 days are evident in Fig. 15.

Discrete groups of P. vitulina juveniles were not commonly found (3.7%) while H. grypus juveniles were more often associated with adults of that species (Table 15, Fig. 17). Juvenile and adult age groups were the predominant ones for the Harbour Seal, whereas the adult age groups, which were next in frequency for this species, were the most frequently observed Grey Seal groups (Fig. 17 & Table 15).

No general pattern is evident in the daily mean number of adults in a group (Fig. 17) except that of a small isolated group that was reasonably constant throughout the study period. Adults of both species were always the last individuals to leave the base site when rising tides began submerging them. Hence these adults were recorded as separate groups during each daily or bidaily increasing tide observed. Aberrant peaks on days 14 and 86 (Fig. 17) were caused by

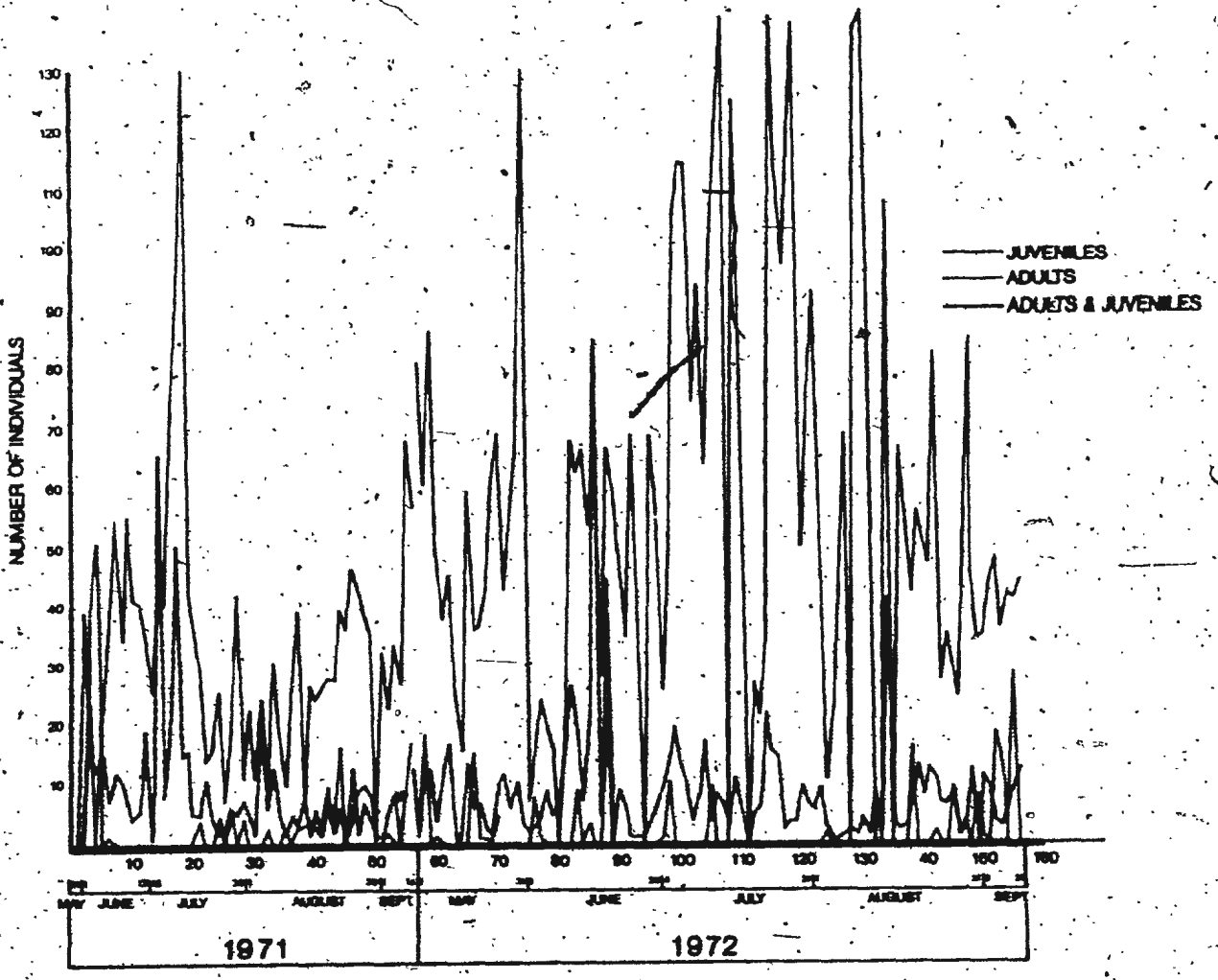

Fig. 17 Daily Mean Number of Seals in Groups Comprised of Juveniles, Juveniles and Adults, and Adults

large groups of adults remaining on the base site during a rising tide, but departing quickly after the observation, hence reduced group numbers were not present at the next observation to lower the illustrated means.

Correlations

The list of variables included in the correlation matrix is presented in Table 16. Table 17 presents the significant correlation coefficients with their associated probabilities obtained from the correlation matrix.

A Pearson product-moment coefficient was used for interval or ratio data and a Spearman's rank coefficient was used for the ordinal data (Ferguson, 1966). Because of the very large N (3883) used to calculate the correlation matrix, very small coefficients were statistically significant, although they accounted for less than 1% of the variance in a particular relationship. In order to delete such trivial correlations, it was decided to increase the acceptance level of significance to $P.<.001$. Correlation coefficients not reaching this criterion, but which are significant ($P.<.05$) are presented in Table 27, Appendix. Correlation coefficients discussed here were significant at the $P.<.001$ level.

An inverse relationship was found between disturbance of the seal aggregations and the rate of haulout (rho = -0.10). Aggregations exposed to disturbance did not emerge onto the sand banks.

Table 16

List of Variables Used in the Correlation Matrix.

Variable
1. Disburbance
2. Hour of observation
3. Air temperature
4. Sea temperature
5. Wind speed minimum
6. Wind speed maximum
7. Cloud cover
8. Tide status
9. Tide height
10. Haulout location
11. Group span minimum angle
12. Group span maximum angle
13. Group number
14. Group density
15. Species
16. Sex
17. Age
18. Haulout rate
19. Tide rate
20. Occupied distance

Table 17

Significant Correlation Coefficients Obtained from the Correlation Matrix.

Variables	Correlation Coefficient
Disturbance & haulout rate	rho = -.10*
Observation hour & wind speed minimum	rho = .12
Observation hour & wind speed maximum	rho = .15
Air temperature & sea temperature	r_{xy} = .67
Air temperature & cloud cover	r_{xy} = -.11
Air temperature & haulout location	rho = -.12*
Air temperature & group span minimum	r_{xy} = .24
Air temperature & group span maximum	r_{xy} = .25
Air temperature & group number	r_{xy} = .14
Air temperature & species	rho = .22
Air temperature & sex	rho = .23
Air temperature & age	rho = .12
Air temperature & group density	r_{xy} = .10
Sea temperature & haulout location	rho = -.12
Sea temperature & group span minimum	r_{xy} = .16
Sea temperature & group span maximum	r_{xy} = .17
Sea temperature & group number	r_{xy} = .15
Sea temperature & species	rho = .19
Sea temperature & sex	rho = .16
Sea temperature & tide status	rho = -.12

*P.<.001 for all correlation coefficients.

Table 17 - (cont'd)

Variables	Correlation Coefficient
Sea temperature & tide height	$r_{xy} = -.17$
Wind speed minimum & wind speed maximum	$r_{xy} = .96$
Wind speed maximum & cloud cover	$r_{xy} = .10$
Tide status & tide height	rho = .31
Tide status & haulout rate	rho = .19
Tide status & tide rate	rho = -.33
Tide height & group span minimum	$r_{xy} = .11$
Tide height & group span maximum	$r_{xy} = .10$
Tide height & haulout rate	$r_{xy} = -.14$
Tide height & tide rate	$r_{xy} = .35$
Haulout location & species	rho = -.11
Haulout location & sex	rho = -.10
Group span minimum & group span maximum	$r_{xy} = .99$
Group span minimum & species	rho = .27
Group span maximum & species	rho = .22
Group span minimum & sex	rho = .12
Group span maximum & sex	rho = .17
Group span maximum & age	rho = .16
Group span minimum & group density	$r_{xy} = .16$
Group span maximum & group density	$r_{xy} = .22$
Group span maximum & group number	$r_{xy} = .20$
Group number & species	rho = -.32

Table 17 - (cont'd)

Variables	Correlation Coefficients
Group number & sex	rho = .36
Group number & age	rho = .59
Group number & occupied shore distance	r_{xy} = .72
Group number & group density	r_{xy} = .61
Species & age	rho = -.26
Species & occupied shore distance	rho = -.28
Species & group density	rho = -.18
Sex & age	rho = .55
Sex & occupied shore distance	rho = .33
Sex & group density	rho = .45
Age & occupied shore distance	rho = .49
Age & group density	rho = .52
Haulout rate & tide rate	r_{xy} = -.33
Occupied shore distance & group density	r_{xy} = .31

Observation hour was positively correlated with wind speed maximum and wind speed minimum (rho = 0.12 and 0.15 respectively). Winds tended to increase in velocity from 0900 to 1700 hours daily.

Air temperature was positively related to sea temperature (r_{xy} = 0.67) but negatively related to cloud cover (r_{xy} = -0.11). The warmest days were those with clear skies. Air temperature was negatively correlated with haulout location (rho = -0.12). This was predominantly a seasonal effect since sites 3, 4 and 5 were only utilized during the warmest periods of the study. Air temperature was correlated positively with group span minimum angle (r_{xy} = 0.24), and group span maximum angle (r_{xy} = 0.25). These correlations reflect the movements of seals to more easterly locations on the Grand Barachois sand banks toward the warmer days of mid to late summer. As air temperature increased, so did the number of individuals in a group (r_{xy} = 0.14). This was a daily as well as a seasonal effect. The positive correlation between air temperature and species (rho = 0.22) indicates the tendency for H. grypus to emerge onto the sand banks some time after P. vitulina, and in greater numbers later in the summer of both years of the study period. The positive correlation of air temperature with sex (rho = 0.2) illustrates a seasonal effect whereby, in the cooler spring, groups of pupping females and groups of males exist, which aggregate in the later summer when

higher temperatures are evident. There was a positive relationship between air temperature and age (rho = 0.12) which reflects the fact that younger groups of P. vitulina pups became assimilated into larger and older aggregations as they were weaned. In early spring, there were low temperatures when pup groups were present at the Grand Barachois. Finally, air temperature was positively correlated with group density (r_{xy} = 0.10). This relationship suggests a very obvious seasonal phenomenon of animals forming closer aggregations during the warmer weeks of the study period. Seal groups were also more densely populated on hot days as previously noted.

Since sea temperature was found to be positively related to air temperature (r_{xy} = .67), many of the above relationships held also for sea temperature. Sea temperature was negatively related to haulout location (r_{xy} = 0.12). As with air temperature, sea temperature rose as the lower numbered sand banks were used more consistently during mid and late summer. Sea temperature was positively related to group span minimum angle (r_{xy} = 0.16) and to group span maximum angle (r_{xy} = 0.17) indicating the same seasonal effect as noted previously for air temperature. Group number was positively correlated with sea temperature (r_{xy} = 0.15), suggesting both a daily and a seasonal effect. Sea temperature was positively related to species (rho = 0.19), indicating that high sea temperatures in the Grand Barachois, character-

istic of falling and low tides, were conditions under which H. grypus (code 2) hauled out, while P. vitulina (code 1) inhabited base sites earlier in the decreasing tide phase and later in the cooler waters of an increasing tide phase than did H. grypus. The positive correlation between sea temperature and sex (rho = 0.16) illustrates a seasonal phenomenon in which females and females with pups frequented the sand banks in early summer, while these same groups were assimilated into other aggregations of males and females during the late summer. Sea temperature was correlated with two variables that were not related to air temperature. Sea temperature was negatively related to tide status (rho = -0.12), indicating a daily effect in which falling or lowering tides were the times at which water had been in the shallow barachois longest and had been influenced by solar heat. Hence the temperatures were highest at those times. Increasing or high tides involved flooding the barachois with cold sea water. This same explanation accounts for the negative correlation between sea temperature and tide height ($r_{xy} = -0.17$).

An obvious positive correlation was found between wind speed minimum and wind speed maximum ($r_{xy} = 0.96$).

The percentage of cloud cover was found to be greater during high winds, such as in storm conditions ($r_{xy} = 0.10$).

Tide status and tide height were positively related since the highest code number for tide status was assigned to high tide (rho = 0.31). Tide status was also

positively correlated with haulout rate (rho = 0.19), since the lowest code number for tide status was assigned to low tide when the great majority of seal aggregations had already emerged onto the sand banks, hence haulout rate was low. Tide status and tide rate were negatively related (rho = -0.33). The tide rate was greater at the times when seals were emerging during a falling tide than when they were re-entering the water during a rising tide.

The positive correlations between tide height and group span minimum (r_{xy} = 0.11) and tide height and group span maximum (r_{xy} = 0.10) confirm the frequently observed phenomenon of seals aggregating on the highest, and thus first exposed, sand bank near the East (Station 0) and generally spreading out to the West more extensively than to the East. Hence, as tide fell, the radian value of group span minimum and maximum did also.

Rate of haulout was negatively correlated with tide height (r_{xy} = -0.14). This relationship illustrates the rather constant attribute of haulout, that it occurred most rapidly when tide heights lowered.

Tide rate was greater at times of seal observation when tide height was approximately 1/3 decreased or 2/3 full. The correlation between these two variables (r_{xy} = 0.35) indicates that as tide variation went through its monthly cycle, the greatest tide rates were on those days when tidal extremes were largest.

The relationship between the two categorical variables, haulout location and species (rho = -0.11) may be clarified by reference to the nominal codes used for each class of these variables (See Table 7). This correlation may be explained by the fact that H. grypus was sighted only on one sand bank (Station 0) whereas P. vitulina was observed on four other base sites as well (See Fig. 2). Haulout location was also related to sex (rho = -0.10) in that groups of seals composed of adult and juveniles of both sexes almost exclusively occupied Station 0 and occasionally Station 2 (See Fig. 2) whereas females and females with young were more variable in their choice of haulout site.

Group span minimum and maximum were very highly related as would be expected (r_{xy} = 0.99) since they are dependant on each other. Both of these variables were positively correlated with species (rho = 0.27, with gp. span max.; rho = 0.22, with gp. span min.). These associations were evident in that groups of seals composed of pups and their dams, which were all P. vitulina, commonly were found more on westerly sites than other groups which included H. grypus.

Sex was related positively to group span minimum (rho = 0.12) and to group span maximum (rho = 0.17). Groups composed of two sexes were more evident to the East of the sand banks than those comprising individual sexes.

Group span minimum was positively related to age

(rho = 0.16) showing that groups comprising conglomerate age classes more frequently inhabited eastern extremes of all base sites, and site 0 in particular, than groups comprising individual age classes.

Group density was positively correlated with group span minimum (r_{xy} = 0.16) and with group span maximum (r_{xy} = 0.22), indicating that as groups increased in size to the East, their animal density increased slightly more than when expansion occurred to the West.

Group number varied positively with group span maximum (r_{xy} = 0.20) which corroborated the previous two correlations. It is of note that group number did not vary inversely with group span minimum.

There were always more P. vitulina than H. grypus at the study site as illustrated by the negative correlation between group number and species (rho = -0.32). There were also typically more individuals in groups of males and females than in groups composed of either sex class independently (rho = 0.36). More individual seals were present in groups comprising all age classes or any two in combination, than any age class independently (rho = 0.59).

Group number varied directly with the curvilinear shore distance that the group occupied (r_{xy} = 0.72). Thus the space groups occupied was increased with greater group numbers. A positive relationship existed between group number and group density (r_{xy} = 0.61). Although large areas of the

sand bank were exposed periodically in the Grand Barachois, animals tended to aggregate in dense groups. The fact that species and age were negatively correlated (rho = -0.26) reflects the fact that H. grypus groups were typically composed of juveniles, or adults and less frequently combinations of these, the code numbers of which were higher than those of single age groupings. That species and occupied shore distance were negatively related (rho = -0.28), illustrates the fact that P. vitulina always had larger group numbers, and these required more space than the much smaller groups of H. grypus. The relationship between species and group density (rho = -0.18) was probably due to the large size of H. grypus resulting in less dense aggregations than those of P. vitulina.

The relationship between sex and age (rho = 0.55) was a meaningless one, although strong, and involved all or most composite age groups containing both sexes. Sex was positively correlated with occupied shore distance (rho = 0.33). Male and female groups usually contained more individuals, and thus took up more space, than groups of exclusively either sex. The same reasoning can account for the correlation between sex and group density (rho = 0.45).

The higher number codes of groups containing pups, juveniles and adults accounts for the high correlation between larger groups and occupied shore distance (rho = 0.49). This reason also accounts for the high correlation between age and

group density (rho = 0.52). Pups only, or females and pups, were usually spread out within their discrete aggregations. Dams with their young were frequently observed in groups where a 10 m. separation distance existed between maternal pairs. Juveniles and adults during the later weeks of the study period increased the density of their groups.

Haulout rate was negatively correlated with tide rate, (r_{xy} = -0.33), showing that haulout was most rapid during periods of the rising and falling tides when currents within the barachois were relatively slow. These times occurred typically at 1/4 to 1/3 lowering tides and 2/3 to 3/4 rising tides.

A negative correlation between occupied shore distance and group density (r_{xy} = -0.31) may be interpreted as larger groups being more dense (as in early to mid August), and larger density groups requiring more space for their haulouts.

Regression analyses.

Regression analysis was performed for all behavioural variables: group span minimum, group span maximum, group number, species, sex, age, haulout rate, occupied shore distance, group density and haulout location. All variables (See Table 16) were entered as possible predictor variables.

A stepwise regression analysis method was used since it consists of a method of selecting variables that provide the best possible prediction of the criterion with the fewest independent variables (Nie, Bent & Hull, 1971). In this method, the first variable selected provides the best prediction of the criterion variable of all variables entered. Variables are then added to this one in the order in which they add a significant contribution to the prediction of the criterion in conjunction with the first one selected. Hence variables are only selected if they contribute a significant amount to the prediction of the criterion. Variables are selected also in the order of the magnitude of this contribution to prediction.

The very large number of observations (3883) involved in calculating the regression analyses led to extremely small variance predictions being statistically significant ($P.<.05$). Hence, the acceptable significance level was increased to $P.<.001$). Only variables reaching this criterion are included here. The multiple correlation coefficient (R) and the variance accounted for (R Square) are cumulative in order of presentation.

Group span minimum. In regression analysis of the criterion variable, group span minimum, 13% of the total variance was predicted by four variables (Table 18). The most important predictor variable of group span minimum was species (RSq = 0.73, F = 306.71). Both H. grypus and P. vitulina showed preferences for precise areas on the base site during the study period. Air temperature contributed 3.3% to the prediction of group span minimum (RSq = .106, F = 230.83), and was the second important factor determining the criterion. A further 1.5% was contributed to the prediction of the criterion by age (RSq = .121, F = 177.20). Young animals hauled out onto the sand banks consistently to the West of their elders. Tide height added .9% to the prediction of the variance of group span minimum (RSq = .130, F = 145.10) which was interpreted as signifying the relationship of seal aggregations spreading to the West as banks were exposed by falling tides.

Group span maximum. The regression analysis of the criterion group span maximum indicated the important predictor variables to be the same as for group span minimum (Table 19). These four variables predicted 13% of the criterion variance. Air temperature was the most important predictor in this case (RSq = .06, F = 247.71). Species contributed 2.2% of the variance of the criterion (RSq = .088, F = 187.18). Age added 3.7% to the prediction of the criterion (RSq = .125;

Table 18

Regression Analysis of Group Span Minimum Angle

Variable	Simple R	Multiple R	R Square	F	P
Species	.271	.271	.073	306.71	.001
Air temperature	.238	.326	.106	230.83	.001
Age	.076	.347	.121	177.20	.001
Tide height	.111	.361	.130	145.10	.001

Table 19

Regression Analysis of Group Span Maximum Angle

Variable	Simple R	Multiple R	R Square	F	P
Air temperature	.245	.245	.060	247.71	.001
Species	.218	.300	.088	187.18	.001
Age	.162	.352	.125	184.36	.001
Tide Height	.100	.366	.134	149.52	.001

F = 184.36), and, finally, tide height contributed .09% of the variance of group span maximum. The associations of each predictor variable with the criterion may be seen from the simple R (correlation coefficient) and the discussion of group span minimum, above.

Group number. A total of 40% of the variance of group number was accounted for by three variables (Table 20). The most significant contribution to the prediction of group number was made by age, involving 35.2% of the variance (RSq = 35.2, F = 2109.48). The largest groups were always older animals or groups of older plus young seals. Species accounted for 3.2% of the criterion variance (RSq = .384, F = 1207.72) in that H. grypus consistently formed smaller groups than P. vitulina. Finally, sea temperature contributed 1.9% to the predicted variance (RSq = .403, F = 871.13), which denoted a seasonal parallel of increasing temperatures with the more complete terrestrial aggregation of pinnipeds in the Grand Barachois.

Species. A total of 25.1% of the variance of species was accounted for by the four predictors in Table 21. Group number predicted 10.5% of the variance of species (RSq = .105, F = 455.73). Larger groups could be reliably predicted to be P. vitulina. Group span minimum accounted for 8.6% of the variance (RSq = .191, F = 458.36). Air temperature added 4.5% to the variance predicted (RSq = .236, F = 398.60) and only 1.5% was accounted for by haulout

Table 20

Regression Analysis of Group Number.

Variable	Simple R	Multiple R	R Square	F	P
Age	.593	.593	.352	2109.48	.001
Species	-.324	.619	.384	1207.72	.001
Sea Temperature	.151	.634	.403	871.13	.001

Table 21

Regression Analysis of Species.

Variable	Simple R	Multiple R	R Square	F	P
Group Number	-.324	.324	.105	455.73	.001
Group span minimum	.271	.437	.191	458.36	.001
Air Temperature	.224	.485	.236	398.60	.001
Haulout location	-.107	.500	.251	324.41	.001

location (RSq = .251, F = 324.41), P. vitulina groups were most frequently of sufficient size to be spread farther to the West than the H. grypus groups, hence species could be predicted by group span minimum. Higher air temperatures during the day were always correlated with the presence of H. grypus, and this predictor could account for the presence of Grey Seals. Haulout locations of sites 1-4 were only occupied by P. vitulina, hence it could be predicted from the base site locus, which species was present.

Sex. Four variables accounted for a total of 28.1% of the variance of sex (Table 22). Group density was the primary predictor of sex, accounting for 20% of the criterion variance (RSq = .200, F = 965.82). Female groups were commonly very dispersed whereas groups of males or both sexes were consistently closely aggregated. Occupied shore distance predicted 4.2% of the variance of sex (RSq = .242, F = 617.98). Male plus female groups, due to their larger size and greater numbers could be recognized as such by the measurement of occupied distance. Air temperature predicted 3.3% of the total criterion variance (RSq = .275, F = 490.95). Early summer was the only time that females or females with pups were observed as exclusive groups, and low temperatures were typical of this period. Only .6% of the variance of sex was accounted for by group number (RSq = .281, F = 379.20).

Age. Three predictor variables accounted for a total of 41% of the variance of age (Table 23). Group number

Table 22

Regression Analysis of Sex.

Variable	Simple R	Multiple R	R Square	F	P
Group density	.446	.446	.200	965.82	.001
Occupied distance	.333	.492	.242	617.98	.001
Air Temperature	.231	.525	.275	490.95	.001
Group Number	.357	.530	.281	379.20	.001

Table 23

Regression Analysis of Age.

Variable	Simple R	Multiple R	R Square	F	P
Group Number	.593	.593	.352	2109.48	.001
Group density	.520	.626	.392	1252.73	.001
Occupied shore distance	.485	.641	.410	899.60	.001

contributed most to the variance (RSq = .352, F = 2109.48). Larger groups were usually combinations of all or predominantly older age classes. Smaller groups were typically young or maternal pairs. Group density predicted a further 4% of the variance (RSq = .392, F = 1252.72). The less dense groups, again, were usually maternal pairs or pups while denser groups were older animals. A further correlate of group number, occupied shore distance, accounted for 1.8% of total criterion variance (RSq = .410, F = 899.60). Groups occupying the greater shore line distances were usually combinations of age classes.

Haulout rate. Regression analysis of haulout rate showed that two variables only predicted a significant amount of the variance of this variable (Table 24), totalling 12.2%. Tide rate was the best predictor of haulout rate, accounting for 11% of the variance (RSq = .112, F = 490.36). Though not an often observed phenomenon, disturbance accounted for a further 1% of the variance of haulout rate (RSq = .122, F = 270.21). Haulout, then predictably increased at times of slight tidal change such as 1/4 decreasing tides or 3/4 increasing tides. During large tide rate conditions, i.e. mid tides, most of the inhabiting seals had emerged to the base site. At times of disturbance, emergence rates onto the sand banks were greatly reduced.

Occupied shore distance. Three group composition variables accounted for 27.4% of the variance of occupied

shore distance (Table 25). Age best predicted occupied shore distance (RSq = .235, F = 1194.53) for reasons stated previously. The next predictor was species, which accounted for 2.8% of the variance (RSq = .263, F = 692.20). *P. vitulina* groups usually spanned greater distances on the sand banks than did *H. grypus* groups. Sex contributed 1.1% to the variance predicted (RSq = .274, F = 692.20). Groups comprising males and females required greater distance spans due to their larger group numbers than groups of exclusively one sex.

Group density. Two predictors accounted for 31% of the total criterion variance of group density (Table 26). Age accounted for the majority of predicted variance (RSq = .271, F = 1440.73). Lower age groups commonly were rather widely dispersed before being assimilated into adult and older juvenile groups. The latter groups typically were very dense with approximately 0.5 - 1.5 m. between individuals. Sex predicted 4.9% of the variance in group density (RSq = .310, F = 862.90), which confirms the observed phenomenon of widely spaced pre and post parturient females as opposed to closely aggregated adult male or male-female juvenile groups.

The only variable analysed by regression that could not be adequately accounted for by any of the recorded variables was haulout location. The three best predictors (sea temperature, species and group number) of this criterion

Table 24

Regression Analysis of Haulout Rate

Variable	Simple R	Multiple R	R Square	F	P
Tide Rate	-.335	.335	.112	490.36	.001
Disturbance	-.100	.350	.122	270.21	.001

Table 25

Regression Analysis of Occupied Shore Distance

Variable	Simple R	Multiple R	R Square	F	P
Age	.485	.485	.235	1194.53	.001
Species	-.285	.513	.263	692.20	.001
Sex	.333	.524	.274	488.35	.001

Table 26

Regression Analysis of Group Density

Variable	Simple R	Multiple R	R Square	F	P
Age	.520	.520	.271	1440.73	.001
Sex	.446	.555	.310	862.90	.001

accounted for less than 5% of the total variance (RSq = .036). Haulout location could not be accounted for by any of the recorded variables in this study.

Life Table of Crucial Activities of P. vitulina.

After two summers at the observation site, it was possible to construct a life table of the crucial periods in the annual cycle of the Harbour Seal (Fig. 18).

Halichoerus grypus, though resident at the Grand Barachois, has not been reported to breed there. Moreover, the study period for this work was not sufficiently extensive to incorporate the typical breeding times of this species, as reported from other areas of the Canadian east coast. During this study, the Grey Seal exhibited a relative constancy of colony numbers, haulout rate and position, and group density. A life table could not be constructed for this species since it was only seasonally present at the study site.

General description of haulout behaviours during pre-pupping. In the last year of the study (1972), observations commenced at the Grand Barachois on May 1. This was approximately three weeks before the sighting of the first viable pup on May 22. Dead ones were noticed as early as May 11 of 1972 and May 5 of 1970. During the pre-pupping period, population levels were very low (Fig. 10) and only adult and juvenile P. vitulina and adult H. grypus were present at the base site 0. These two species had proximate groups but were not intermixed, and group density for the Harbour Seal was at the rather constant level typical of pre-pupping and post-moulting (1.35 seals/m.). These animals emerged from the water when tide recession exposed

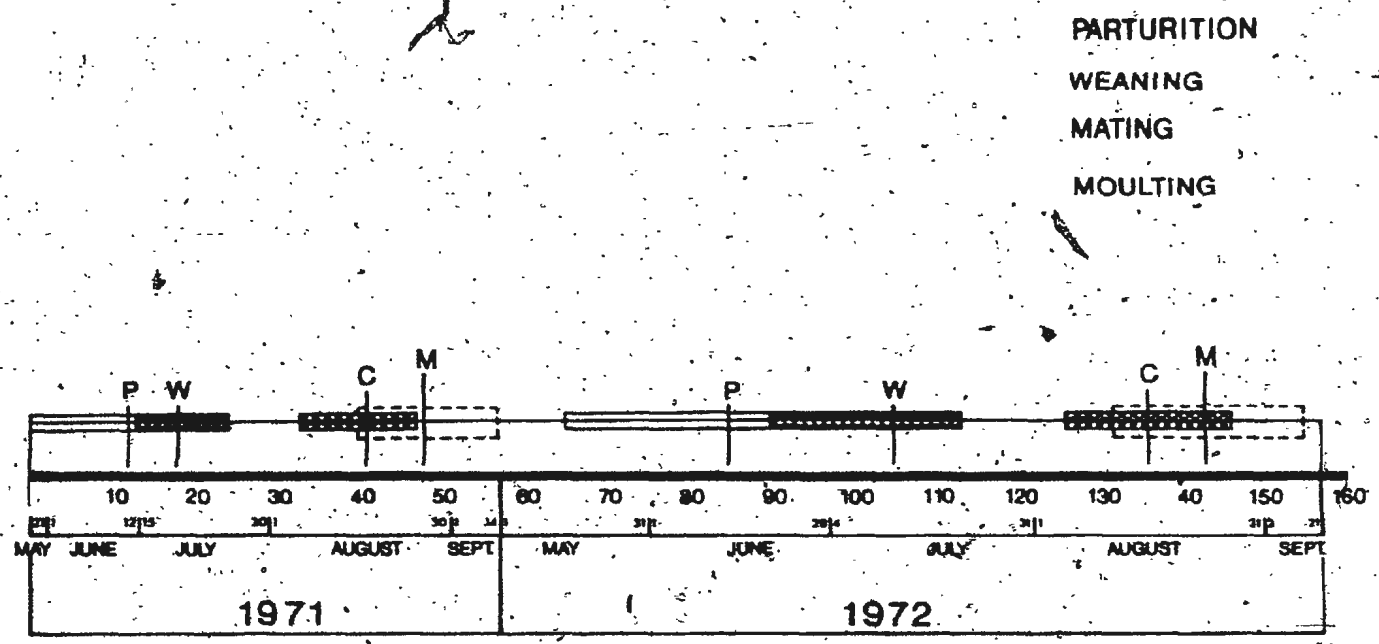

Fig. 18 Life Table of Phoca vitulina at the Grand Barachois Miquelon

their terrestrial sand bank base site and remained as long as 10 hours between the first emerged and the last to submerge. As stated previously, young animals or juveniles often initiated the haulout after a disturbance by coming onto the bank and re-entering the water several times. Finally these individuals emerged for a length of time and other, older animals followed. Generally adult seals of P. vitulina were the first animals emerged and the last to leave the base site. Their preferred site was thus the highest point of the sand bank in the barachois and some segregation of ages within a group was consistently observed. (Fig. 19).

Group numbers increased from the haulout commencement until ½ to 2/3 increasing tide occurred, after which seals left their base site and group numbers decreased evenly but rapidly. Both species of seals closely inspected their sand bank area, on which they finally emerged from the water, prior to hauling out. Inspections were often protracted while the animal was carried past the haulout site in tidal currents and viewed it from a 20 meter distance. Often a seal group in the water would pass up channel from an imminent base site in order to drift slowly past the area.

Seals always faced inland when hauling out and initially remained so. The first animals to emerge remained within a group and were quite stationary, exhibiting a posture of just emerged seals. This posture consisted of a raising

Fig. 19 Aerial View of Pre-pupping Seal Distribution

and fanning of the rear flippers at a 70-80° angle from the sand bank and the head and neck in the same manner. This behaviour has not often been explained, although a thermoregulatory function has been noted of the rear flippers in this species (Tarasoff & Fisher, 1970). Another possibility is that ectoparasites are commonly found in the anal, axial regions and in the folds of the neck epidermis and dessication of these organisms may remove them. Initial emergent seals did not move very far inland on the sand bank, although new areas of bank were tidally exposed for successive animals.

This mechanism, it seems, provides an appropriate interpersonal distance between animals that is maintained until the tide once more starts to rise. Rising tides often induced intraspecific strife in both P. vitulina and H. grypus over space on the highest portions of Site 0. These disputes were more frequently conducted between juvenile males of H. grypus than adults and between adult males in P. vitulina. If insufficient distance was present between an animal hauled out and a newcomer landing on the sand bank perimeter, the resident animals repelled the intruder with mild warning by fore flipper waving and scratching, closed or open mouth head thrusts or charges in extreme cases. The intruder, if persistent, then obtained a portion of sand bank between the external periphery of the seal aggregation and the water. These areas were preferred to going to the

ends of the group, which was spaced 2-3 animals deep along the sand bank shore. When no adequate space existed within the group span, it was often necessary to go to the ends of the group. Late comers to the sand bank were commonly young seals and new animals hauled out even after the low tide in the pre-pupping period. They assumed a position near the water on either end of the major seal group, or rarely travelled around the group to an inland location. These movements resulted in members on the ends of the seal group always being the most alert animals, since they had not yet settled to doze. The end animals were inevitably the ones to first notice any unusual movements of approaches to the seal group and often the first to re-enter the water in fear. All these interactions and activities as well as a certain amount of rolling, scratching and stretching movements by individuals resulted in a loose aggregation with animals facing in no general direction.

Mild aggressiveness was common within the aggregation and usually took the form of the scratching in mid air behaviour while the animal was lying on one side, or close mouth thrusts from the same position. Generally, however, the pinnipeds were quiet and resting for most of their time on shore. The seals slept for 20-50 minutes, then awoke to move slightly, or stretch and scan the horizon, rather than sleeping for long periods of time. They seemed at all times to be responsive to splash sounds

indicating some member of the aggregation fleeing, or other sharp reports, even during sleep. As mentioned in other studies (Bishop, 1967), Harbour Seal groups could be approached very closely by crawling on one's ventral surface along the haulout area. Using species specific postures, as raising the rear legs seemed to alay fear in the peripheral members of the group. These animals never slept during such an approach, though closing the eyes, lowering the head and resting for a maximum of 4 minutes was observed. Objects or individuals approaching along the shore of the sand bank were less disturbing to the watchful seals than overland approaches, which inevitably resulted in a herd stampeding.

Parturient and post-natal haulout behaviours.

The parturition of viable pups was first observed on May 22 at the Grand Barachois and followed the same pattern as described by Bishop (1967) and Klinkhart (1962). Some annual variations in mean pupping date for this species has been reported by Boulva (1972) at Sable Island. Insufficient data were available from this study to determine if this effect occurred at Miquelon. Stillborn or deserted P. vitulina pups were prevalent during May, and were collected on May 11, 24, and June 3, 1972. The average weight of these slim animals was 8.2 kg., the smallest being 6.35 kg., and their stomachs were empty.

On May 23, 1972, a day after the sighting of the first viable pup, a split of the normally compact group of

seals was evident. Some adult females with pups moved to the western extreme of the exposed Banc au Monsieur (Site 0, 20-25°) quite apart from the originally compact aggregation at 55-75° magnetic. The parturient and suckling group enlarged daily and reached 40 dams with pups by May 26, 1972.

Pups were motile at birth but did not suckle immediately, waiting 10-25 minutes to do so. All seal births observed were on land, and placentas were often noted scattered on the sand in the early morning, before tides or gulls, Larus marinus and Larus argentatus, removed them. The suggestion of previous authors (Scheffer & Slipp, 1944) that birth may occur in the water due to placentas floating in unlikely places, was not confirmed in this study. Pups were never left unattended during their first week after birth but thereafter, pups in groups were observed on sites 1 and 0 west. Pups suckled almost immediately upon emerging from the water with their dams, a process which was always directed by maternal scratching of the pups' nosing head until it found the teat. Suckling usually lasted 3-12 minutes, after which the dams sometimes left the more elderly pups and returned to the water. Suckling and pupping groups were not usually in evidence on the sand banks before a large aggregation of adult males and juveniles had hauled out on Site 0 east. A maximum number of pups (104) were observed on day 107, this formed 22% of the post-parturient maximum population of 423 animals.

June 14, 1972 was the mean pupping date for P. vitulina on Miquelon. This further complicates Bigg's (1969) synthesis of clines in the pupping season of this species. Pupping dates on Sable Island range from May 22-28, 1970-72 (Boulva, 1972).

By July 18, 1972 the western pupping area on Site 0 and the southern pupping area (Site 1) which were utilized from May 29 to July 7 were deserted. Sites 2 and 3 were utilized from June 3 to July 6, 1972 by dams and pups, though not as frequently or extensively as the other two pupping and suckling sites. (Fig. 2). The greatest number of pups and dams in a single group was 96 on July 16, 1972, and peak numbers were evident just previous to the desertion of the pupping areas on July 18. On this date, the earliest pup born had fish in the gut. This 30 kg. animal was obviously weaned. Weaning occurred at the time when exclusively dam and pup haulout groups disintegrated. Weaned pups were observed feeding on July 10, 1972 and at that time capelin were present in la Goulet de Langlade (July 10-20 in 1971-72).

Play behaviour between pup and dam, observed before weaning, consisted of rolling and harmless nipping with general emphasis on tactile contact. Dams would direct the swimming pup if it was chased by a boat. Pup and dam would swim away from the pursuer parallel to one another, and sharp

turns would be negotiated by the pair in perfect synchrony, the mother leading slightly and turning the pup with the contact of her torso and nearest fore-flipper.

Haulout after pup weaning. After weaning, pups were very curious of human activities on nearby beaches or in stationary boats. At the age of 3-5 weeks when weaning occurred, pups were essentially forming groups of that age class exclusively, but only because they still frequented the pupping areas though they were unattended by their dams. Postweaning play behaviour consisted of leaping out of the water porpoise style, or rolling on the surface and slapping it with the fore flippers, making a sharp 'cracking' sound, which occasionally stampeded small groups of hauled out juveniles and pursuant adults. When tide height increased allowing 20-30 cm. of water to flood areas of the sand bank near the major adult group (Site 0 east), pups were observed to skim over the bank in shallow water at top speed throwing a spectacular, rooster-tail like spray behind them some 2 - 3 m. in the air. The weaned pups commenced aggregating with the major group of seals before mid July, after which other sites on the Barachois were not utilized. Group density of the pupping and suckling groups was considerably lower than that of the adult aggregation, however, by late June, even these groups were compact.

Breeding haulout and activities. Breeding was first observed on August 5, 1973, and one or two incidents

daily were suggestive of copulation according to the descriptions of Harrison (1960), Venables & Venables (1957;1959) and Bishop (1967). The flat topography of the Grand Barachois did not afford a vantage height of land to permit clear underwater observations of copulation. Breeding activities often involved paired animals rolling, splashing and chasing one another for durations up to 20 minutes. These activities, which may be classed as a form of courtship behaviour, were invariably followed by languid rolling and periodic paired submergence of the two animals, uniquely characteristic of copulation in P. vitulina. This latter behaviour lasted up to 15 minutes and consistently occurred near dusk and during rising tides. Typical of the whole period of breeding, during which behaviours described above were observed eight times, was the noticeable addition of canid-like howls and snarls coming from Site O (east) during 3/4 increasing tides at night or during the day. These sounds could be correlated with increased aggressiveness between males, as well as general irritability and wariness throughout mating. Male aggression followed the same hierarchy of signals used in maintaining individual distances during the pre-breeding and post-breeding period. However, actual connecting lunges to the opponent's jaw and neck region were more frequent. These attacks were often used on females as well, although the female reaction was usually repellant by waving, scratching or thrusting the head forward toward the intruder and escaping into the water. This type of male-female interaction probably

separated receptive females from those not yet ovulated, although other pinnipeds, ie. Northern Elephant Seal, typically engage in combat as an immediate antecedent to mating. Group density was very high during breeding (Fig. 12) although group numbers dropped considerably. Only the eastern end of Site O was utilized as a base site during this time. The tendency to aggregate the whole colony of seals after weaning is indicated by a large increase in mean group number (Fig. 13).

Moulting aggregations. Moult could not be intensively studied in the pinnipeds at the Grand Barachois, however, a date of peak moulting was arrived at from observations of animals from an 80 meter distance. Fading hair from the typical black or grey coloration to brown with white tips indicated the death of old hair, and bare spots on the axillae and ventral regions were black and leathery in contrast. Dead fur, though in the dermal follicle, became less oily and slick and more stiff and dry. These changes in the fur were best observed in dry animals, as wet seals tended to look sleek, oily and dark, though they were in full moult. On the basis of these observations, and the collection of a few animals, August 12-16 was determined to be the period of peak moult for the Grand Barachois aggregation. Sex differences in the precise timing of moult have been detected in P. vitulina richardi (Stutz, 1967), females show a greater tendency to spread

moulting over a larger time period, perhaps in relation to the timing of post-parturient hormonal events. This study was not attuned to record such information.

Group numbers and the population level decreased in the period after peak moulting and after mating. Group density, which had reached the peak for the study period during moult (2.9 seals/meter), also decreased to a minimum of 0.6 seals/meter. The numbers of seals occupying the sand banks at the Grand Barachois decreased from the middle of August, but were observed to increase during the first week of September and October. Observations on the pinnipeds were terminated prior to mid October in both 1971 and 1972.

Interspecific Influences on Terrestrial Aggregations of Harbour and Grey Seals.

The Harbour Seal has been described as being among the most sedentary of seals (Scheffer, 1958) Fluctuations in the numbers of both Harbour and Grey Seals utilizing the terrestrial base site at the Grand Barachois were however, frequently observed to be caused by the presence or activity of other biota in the lagoon.

Biotic influences of terrestrial origin almost invariably induced some disturbances in the seal aggregations and often precipitated the groups' entry into the water. The one exception to this was the presence of another pinniped species on a sand bank which tended to induce the emergence of other seals onto the same base site. This was also the case when members of the same species occupied sand bank loci. Interspecific tolerances between pinniped species have been observed previously (Orr, 1965). Moreover, many pinnipeds extend intraspecific proximity and contact tolerances to other species within the order. The presence of one species (P. vitulina) facilitating the haulout of another (H. grypus) has not been reported.

In contrast, aquatic biotic influences such as, the presence of prey species typically caused the aggregation to enter the water in a brisk but orderly fashion. Mass group dispersals to

the water for feeding purposes were not of the same rapidity or disorder that characterized flight stampedes.

The biotic components of the five base sites near Miquelon where seals were observed have been presented. (Table 1, and in the Study Area description). The species number or type did not change significantly from location to location. The major difference was in the molluscan fauna of the Grand Barachois and the other four areas, and the predominance of estuarine eel grass, Zostera marina, in the pupping area. This reflects the sand and mud bottom habitat present only in the Grand Barachois. There were no observations to suggest that the biotic properties of the Grand Barachois, not present in the other haulout areas, were important to the seals resident at the Barachois. Although molluscs have been reported in the guts of both species elsewhere (Spalding, 1964; Templeman et al., 1957), observations did not confirm that seals were using Mya arenaria or Placopecten magellanicus as food stuffs in the Grand Barachois.

The entire aggregation of pinnipeds in the Grand Barachois was observed to re-enter the water from its base sites to feed upon schools of capelin, Mallotus villosus or sea run trout, Salvelinus fontinalis, which appeared during rising tides in mid June and the monthly high tides of July. The specific stimulus prompting the seals to re-enter the water was not evident, although the mass re-entry was not a stampede but a less rapid activity. The

phenomenon was noticed to be preceded by a small number of pinnipeds actually predating these migrant fish resources, which may have been the cue recognized by the terrestrial aggregation 100-300 meters distant from the predation.

Capelin were also plentiful in areas around the other four haulout locations near Miquelon. The more offshore area surrounding Little Green Island was renowned for its copious quantities of ground fish such as cod, Gadus morhua, and haddock, Melanogrammus aeglefinus. All areas were close to large schools of surface migrating teleosts such as mackeral, Scomber scombrus, and herring, Clupea harengus. These species were utilized extensively by the Grand Barachois seals during mid to late summer, and swimming aggregations of both seal species were observed at various points of land around Miquelon jutting out into the main stream of inshore pelagic migrating prey.

Cooperative predation was not observed in either species of seal, although group feeding of the two was not uncommon. Around the northern and western sides of Miquelon individual P. vitulina were sighted, each proximate to one of the many small promontories of rock that jutted seaward and were separated by distances of 200-150 meters from each other and by 10-50 meters from the shore. This spacing phenomenon was surprisingly regular and consistently observed in July and August. Seals of both species were rarely observed inshore near La Dune on the eastern side of Isthme de Langlade except when migrating fish were present, since the sandy bottom

in this area is relatively barren in comparison to the waters off Miquelon and Langlade in which reside numerous ground fish. Grey and Harbour Seals were only seen near L/Isthme in proximity to la Goulet de Langlade, and were then moving to or from deeper waters.

As is typical of the order, both species were observed to be opportunistic feeders. The staple diet was ground fish, with occasional meals of lobster, Homarus americanus, and spring forages of capelin, in or around the Grand Barachois. Numerous sculpin of the long and shorthorn varieties, and skates, Raja sp. were found drifted onto the beach after being eviscerated. It was perhaps the proximity to quantities of ground fish in August of 1971,1972 that induced a decline in seal numbers at the Grand Barachois in favor of the other haulout sites. Food presence, then, did influence the numbers of seals on the base site in the Grand Barachois.

Other biotic influences on the seals were the disturbances caused by various terrestrial species, horses, bovids and man. Farm stock, by their rapid movement caused the seals to flee at Pte. aux Cacaouis near the major haulout site 0. This occurred as a chain reaction in the seal aggregation. H. grypus always reacted first to a disturbance. The flight distance for this species was approximately 100-500 meters, whereas the usual flight distance of P. vitulina was 50 meters at the study site. The

latter species was approached by boat to a 10-20 meter distance before entering the water. At two periods of the year, P. vitulina and H. grypus show no or little tendency to re-enter the water when approached. These times were pupping in both species and moulting in P. vitulina. Females of both species have been observed by the author to stay near their pups rather than escape to the water when approached.

The seal aggregations were also disturbed by small boats. People travelling by boat in the channel near Pte. aux Cacaouis rather than the channel near Site O, caused little disturbance although the passing craft was constantly watched by the seals. Rapid acceleration of auto or boat motors, sharp reports as shouts, gunshots, or striking a resounding object, often induced seal flight from the sand banks, though the source of the stimulus for flight was not visible to them. Inanimate objects such as floating steel drums or rubber rafts in the tidal currents near the seal group, or small aircraft diving over the animals often stampeded the seals to the water. Pups from birth were quite prepared to follow their dams into the water when frightened, but were somewhat less adroit. Females were observed to emerge from the water more readily after a disturbance when their pups had remained ashore. Thus pups appear to be a strong incentive for dams to haulout.

Any disturbance significantly reduced the seal

haulout rate. Disturbed animals either 1, went into the water near the occupied base site and waited until the disturbance passed 2, went through the Goulet, in small numbers or larger numbers, if the disturbance was great or followed them (ie. a boat) 3, if pursued, swam or porpoised towards the North or Northwest to enter the large inland bay of the Grand Barachois, or if the disturbance was stationary or brief, emerged onto the West end of the bank. H. grypus when disturbed usually exhibited 2 while P. vitulina, particularly during the time of moult, frequently exhibited 1 and 3 above.

The only birds directly affecting the Grand Barachois pinnipeds were scavengers. The Herring Gull, Larus argentatus, and the Great Black-backed Gull, Larus marinus, did not appear to induce mortality in the seals. They utilized only placentae and cadavers. These birds, as well as Larus delawarensis, the Ring-billed Gull and Sterna hirundo, the Common Tern, often fed with the seals on capelin in late June.

During mid to late August schools of Common Porpoises, Phocoena phocoena were observed feeding in la Goulet de Langlade. Seals were never present when the cetaceans occupied the channel.

Discussion

The phenomenon of haulout involves the interaction of seals with land or ice and water. Based on historical data, it was assumed that the regularity of haulout in Phoca vitulina and Halichoerus grypus precluded that behaviour being achieved in a random fashion. Indeed some of the factors shown to influence the characteristics of seal haulouts on preferred base sites in previous studies, were investigated in the present one.

There were four general classes of possible influences on haulout examined on or near the Grand Barachois base site. These were the biotic and physical elements of both the terrestrial base site and the proximate marine habitat, including the changes of each during the study period.

Biotic factors were classed as either intraspecific or heterospecific. The former was described in the Life Table of P. vitulina (p.112) and the latter separately. (Description of Study Area p.21). Physical influences on the seal aggregations were topographic (reported in the Study Site p.21) and climatological (reported in the Results p.42).

The topographic conditions in which P. vitulina were observed had several common attributes, specifically protection from the wave action produced by

prevailing winds in an island lagoon situation when conditions were sheltered such as isolation from human disturbances or terrestrial predators, tidal exposure of utilized shorelines, and proximity to food sources. The only topographical attribute which distinguished the Grand Barachois from other seal haulout sites was the presence of open areas of tidally exposed sand. Open expanses of sand probably provided the seal with sufficient warning of the approach of terrestrial predators. The latter are reduced in the isolated locations characteristic of whelping areas for P. vitulina and in summer foraging locations for H. grypus. This was tested by examining possible terrestrial stimuli that cause seals to leave their base sites. Two characteristics of site) at the Grand Barachois that are unique (Fig. 2) are being the first sand bank to emerge during a falling tide, and thus the last to be submerged during a rising tide, and its proximity to the deepest water channel in the barachois, which itself was the closest to the channel opening to the sea. Hence Station 0 provided two functions; ease of accessibility to or from the sea, and the advantage of the earliest possible haulout sand bank in the barachois. Fishermen confirmed the author's observations that the barachois was the only location of five observed in which Harbour Seals

parturated. Similar locations known to provide pupping sites for that species are Sable Island (Boulva, 1972; Merdsoy, 1973), Burgeo Barachois (Templemen et al., 1957), Skeena River, B.C. (Fisher, 1952) and Tugidak Island, B.C. (Bishop, 1967), all of which provide tidal sand flats.

Grey Seals were observed to haulout only on one base site (Station 0) and exclusively in the Grand Barachois. Considering that H. grypus pups were not observed in the area, Mansfield's (1966) suggestion that Miquelon provides only a summer, non-breeding resting place for the species, and that they are seasonal immigrants from the breeding population on Sable Island seems valid.

Previously it has been reported that the pinniped population of Miquelon was entirely H. grypus numbering approximately 1500 (Mansfield, 1966). Whether these animals have changed haulout loci because of disturbances in the area or whether natural mortality has decreased the seasonal herd is not known. Nevertheless, only 82 H. grypus and 423 P. vitulina now occupy a typical seal habitat at Miquelon.

The topographic conditions of the Grand Barachois were relatively stable during the study period. The attributes of base site habitats preferred by seals could only be investigated by a comparison of a number of haulout areas. Sedentary marine biota were never observed to be utilized in

the other hauling out areas near Miquelon, although the presence of transient or migratory teleosts did affect the seal aggregations.

A causal relationship between feeding and seal dispersals from base sites has not been previously reported. Both P. vitulina and H. grypus were observed to effect total evacuation of their base sites when prey species were present in nearby waters. Only in concentrations of migratory teleost prey were the two seal species observed to feed in groups. More typically, P. vitulina was observed individually patrolling stretches of coastline, rarely in proximity to another seal. The distances between Harbour Seals patrolling the coastline were observed to vary from 200 meters to one kilometer.

H. grypus were observed to feed near the coast of Miquelon only in schools of migrant fish, and are presumed to feed only in deeper water. The smaller Harbour Seal can swim more rapidly than the Grey Seal. The former species with its proven deep diving capacity (Kooyman & Anderson, 1969) would more appropriately predate sluggish offshore ground-fish. This suggestion may be supported by the consistently later daily haulout time of H. grypus, indicating that its feeding areas may not be as close to the Grand Barachois as those of P. vitulina.

Peak weaning of P. vitulina for 1971 and 1972 coincided with the presence of large numbers of capelin in the Grand barachois and along the sea shoreline. The presence of these convenient prey may be an important attribute of seal breeding areas, and the timing of the actual parturition and weaning dates. Long term correlational studies should be done to substantiate this hypothesis.

Both P. vitulina and H. grypus exhibited a very strong site tenacity in the Grand Barachois. Site 0 (Fig. 2) was utilized by 94.5% of the seals. The other sites were almost exclusively occupied by pups and dams of P. vitulina, while H. grypus was never observed at these other sites. The greater occupation of Site 1 in 1971 over 1972 was probably a result of the observers inhabiting cabins near this location after the pupping aggregation had been established in 1971 but prior to its formation in 1972. Pupping P. vitulina groups also caused variation in seal groupings at Site 0. This age class was clearly separated from the adult group of animals 300 meters to the West.

Haulout rates could not be used to separate Grey from Harbour Seals as they did not exhibit different rates of emergence or re-entry at their base sites. This variable might, however, have been different if the number of Grey Seals frequenting the Grand Barachois had equalled that of Harbour Seals. Grey Seals

emerged onto the sand banks in groups, probably reflecting the homogeneous group age composition, whereas Harbour Seals emerged individually but in rapid sequence. This difference may be responsible for the numerical similarity in haulout rates for both species.

H. grypus consistently required a greater space on the base site than did P. vitulina, undoubtedly due to the former's greater size, since inter-organism distances were similar for both species. Groups comprised of both species tolerated each other as if the group were composed of one species. Though a group of Grey Seals was commonly observed in the midst of a larger group of Harbour Seals, they were segregated only by the homogeneity of species and not by distance. Indeed, H. grypus individuals were often noticed to be separated from their species group by a juxtaposed P. vitulina group. The close terrestrial proximity of these two species suggests that little interspecific competition exists for those attributes of the base site which are utilized by these pinnipeds, further, that these attributes are probably the same for both species. Also due to the size differential between the two species, groups of P. vitulina were commonly more compact and denser than those of H. grypus.

The majority of the groups of seals observed were composed of both sexes. However, female groups were much more frequent than male groups since the former separated

from the main aggregation for the purposes of parturition and suckling. Semi-and fully weaned seals continued to use their feeding sites after the mothers had left. This has been reported for H. grypus and Arctocephalus pusillus (Fogden, 1971; Rand, 1967), but has been interpreted as an active separation by the pups from the main body of animals.

Changing biotic influences and environmental variables, such as meteorological and hydrographic influences on the Grand Barachois seal aggregation were studied by comparing the variability in these physical factors with changes in animal groupings.

Air temperature and its strong correlate, sea temperature, were important influences on the behaviour and gregariousness of P. vitulina and H. grypus. The latter hauled out in greatest numbers on the warmer days, but the Harbour Seal's increase in colony numbers was related to seasonal air temperature increases. Though this environmental variable has been suggested as important in the timing of such crucial activities as moult (Rust, 1962), photoperiodic influences are probably the ultimate causal variable (Ling, 1970).

Great changes in the position or location of P. vitulina aggregations varied concommittantly with temperature, as did density of groups, and their composition. Air and water temperature were also influential in and significant predictors of the position of seal groups, their number, sex and species composition.

H. grypus were more numerous at the barachois during warmer days, and the warmer times of each day. P. vitulina exhibited increased haulout numbers in response to warmer temperatures, especially during the period of moult. These behaviours suggest the need of solar radiation input for the dermal reparative and moulting functions in both species. In vivo study of the dermis in the captive animal under emperical conditions or in vitro examinations of dermal and epidermal growth should be attempted to test this prediction.

Curiously, sea temperature was a better predictor of the number of animals within a group than air temperature. This effect was probably due to sea temperature being more regular in its seasonal changes and less variant daily. These same environmental variables have been reported to be important in aggregations of Otaria byronia, Arctocephalus australis and Callorhinus ursinus (Vaz Ferreira & Palerm, 1961; Bartholomew & Wilke, 1956). Overheating in these three species was alleviated by periodic oceanic dips or residing in the shade of rock overhangs sheltered from the sun's rays. These

behaviours were most evident during the hot summer months in the southern species. This phenomenon has been observed in the Walrus, which also basks during clear sunny days in winter (Fay & Ray, 1968). The present study, however, indicated that P. vitulina and H. grypus directly respond to small variations in ambient air temperatures as opposed to escaping intolerable extremes of this parameter. Nothing suggested that the summer aggregation of these species experienced intolerable temperatures at the Grand Barachois.

Neither wind speed nor cloud cover were important variables in predicting the pinnipeds' behaviour, although extremes of either, including gale force winds and heavy precipitation, were known to induce seals to leave the base site.

The status and height of the tide were two variables which were integral to the haulout characteristics of the two species of seals. Seals were very reluctant to emerge from the water on any shore around the Grand Barachois, isolated though it was. Hence, these animals were dependent on the tidal exposure of sand banks in the middle of the lagoon to haulout. Low tides provided the required sand bank area and neap tides often did not submerge all banks to an unusual degree. The seals always abandoned these areas near high tide, except during the periods of moult, when some intraspecific strife was entailed in the retention of base site occupation.

H. grypus was observed in the barachois in small numbers during the months of May to mid June. However, later in the summer months, numbers of this species occupying sand banks increased. This is consistent with the observation of Cameron (1970) who noted this species' preference for land during high tides before early June but during ebb tides after that time. Cameron suggested that this change involves the availability of food during different periods of the year. However, the data presented here suggest that Grey Seals choose the most isolated locations for base sites during the post-moult period, typically areas with insular design or small areas surrounded by water thus subject to tidal exposure. They avoid mainland base sites in keeping with an increased wariness during the summer period, in contrast to the relative oblivion to disturbance exhibited during breeding.

The rate of seal haulout was also correlated with tide height and the tide rate of change, since the largest number of seals to emerge did so while tidal currents or change were minimal. This relationship is probably applicable across the geographic range of the two species, since their habitat preferences are generally consistent. Haul-out rates have not been quantifiably defined for any other pinniped species. Tide rate was also a significant predictor of haulout rate, as was disturbance. The latter, though rarely occurring and causing changes in the immediate haulout pattern,

was not observed to detrimentally or permanently affect the aggregation. Some mortality of young animals may have been caused if repetitive disturbances influenced the colony during parturition. However, mortality induced in this manner would be at least equalled by the natural deaths of newborn pups. The observed stillborn or post-natal mortality of Harbour Seals was only 9% of the total yearly recruitment of the barachois. This species seems quite adaptable to living in the proximity of man, since its precocity at birth and acute senses protect it from most attacks.

The sex and age composition of seal groups, their size and haulout location were unique for each species studied, and any of these variables could be used to predict another.

Air temperature also was a significant contributor to predicting these group composition variables, but it was the only environmental variable to do so. Conversely, group density and occupied shore distance were best predicted by the group composition variables of age, sex and species.

The results of this study confirm the description of P. vitulina as loosely gregarious by Scheffer & Slipp (1944), though this applies only outside the crucial periods of the annual cycle. The importance of the base site area for both species appeared to be related to its isolation from disturbance, relative inaccessibility to terrestrial

predators and the length of time the location was tidally exposed. The presence of available food was also found to influence the haulout activities of both species of seals. Results also suggest the relative imperviousness of P. vitulina and H. grypus to moderations of all meteorological conditions, except ambient temperature, and a close dependence on tidal influences.

More precise information of this kind could be obtained by the refinement of the present technique for the quantitative measurement and description of animal groupings. This could be accomplished by determining the precise age, sex and species of the animals to be studied and individually marking each prior to the commencement of observations. Techniques have been designed to permit mass captures of animals, hence accurate long distance recording of seal group compositions are realistic.

Another possibility is the use of two observers to visually triangulate groups in areas where no reference points, as the sand banks in this study, are available. This would permit the positioning of groups of animals which do not have a linear dispersion as the seals in the Grand Barachois.

Since haulout descriptions only infer the seals' aquatic behaviours and needs, radio telemetric instrumentation could be efficiently used with these animals to monitor their infrequently researched and largely unknown oceanic activities.

References

Backhouse, K.M. 1959. Seals. New York: Golden Press.

Backhouse, K.M. & H.R. Hewer. 1957. A note on spring pupping in the Grey Seal (Halichoerus grypus Fab.). Proc. Zool. Soc. London, 128: 593-594.

Bartholomew, G.A. 1952. Reproduction and social behaviour of the Northern Elephant Seal. Univ. Calif. Publ. Zool., 47: 369-472.

Bartholomew, G.A. 1953. Mother-young relations and the maturation of pup behaviour in the Alaska Fur Seal. Anim. Behav., 7: 163-171.

Bartholomew, G.A. 1954. Body temperature and respiratory and heart rates in the Northern Elephant Seal. J. Mammal., 35 (2): 211-218.

Bartholomew, G.A. & P.G. Hoel. 1953. Reproductive behaviour of the Alaska Fur Seal, Callorhinus ursinus. J. Mammal., 34(4): 417-437.

Bartholomew, G.A. & F. Wilke. 1956. Body temperature in the Northern Fur Seal. Mamm., 37: 327-337.

Bertram, G.L. 1940. The biology of the Weddell and Crabeater Seals with a study of the comparative behaviour of the Pinnipedia. Br. Mus. Nat. Hist. Br. Graham Land Expedition, 1934-1937, Science Report, 1: 1-139.

Bigelow, H.B. & W.C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish. Bull., 74, 53: 1-577.

Bigg, M.A. 1969a. Clines in the pupping season of the Harbour Seal (Phoca vitulina). J. Fish. Res. Board Can., 26: 449-455.

Bigg, M.A. 1969b. The Harbour Seal in British Columbia. Fish. Res. Board Can, Bull., 172: 1-33.

Bishop, R.H. 1967. Reproduction, age determination and the behaviour of the Harbour Seal, Phoca vitulina L. in the Gulf of Alaska. MSc. Thesis, University of Alaska, 1967.

Bouiva, J. 1972. Temporal variations in birth period and characteristics of newborn Harbour Seals. Presented to the Symposium on the Biology of the Seal at Guelph, 1972, 14pp.

Boyd, J.M. 1957. Aerial studies of a breeding colony of Grey Seals, Halichoerus grypus (Fab.) at Gasker, Outer Hebrides in 1955 & 1956. Proc. Zool. Soc. London, 129:333-342.

Boyd, J.M. 1963. The Grey Seal (Halichoerus grypus) in the Outer Hebrides in October, 1961. Proc. Zool. Soc. London, 141:635-662.

Boyd, J.M. & R.M. Laws. 1962. Observations on the Grey Seal (Halichoerus grypus) at North Rona in 1960. Proc. Zool. Soc. London, 1962, 139:249-260.

Boyd, J.M., J.D. Lockie & H.R. Hewer. 1962. The breeding colony of Grey Seals on North Rona (1959). Proc. Zool. Soc. London, 130:257-277.

Burns, J. 1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J. Mammal., 51(3):445-454.

Butler, G.D. & M.D. Udvardy. 1966. Basking behaviour of the Hawaiian Monk Seal on Laysan Island. J. Wildl. Manage., 30(3):627-628.

Bychkov, V.A. & S.V. Dorofeev. 1962. On the behaviour of Fur Seal bulls during the harem period. Zoologischsky Zhurnal, 1962, 41(9):1433-1435.

Caldwell, L.C. & D.K. Caldwell. 1966. Epimeletic (care-giving) behaviour in Cetacea. In Whales, Dolphins and Porpoises. ed. K. Norris, Calif: University of California Press, 1966, 755-788.

Caldwell, D.K., M.C. Caldwell & D.W. Rice. 1966. Behaviour of the Sperm Whale, Physeter catodon. In Whales, Dolphins and Porpoises. ed. K. Norris, University of California Press, 1966, 678-717.

Cameron, A.W. 1967. Breeding behaviour in a colony of Western Grey Seals. Can. J. Zool., 45:161-173.

Cameron, A.W. 1967. The behaviour of adult Grey Seals, Halichoerus grypus, in the early stages of the breeding season. Can. J. Zool., 47:229-233.

Cameron, A.W. 1970. Seasonal movements and diurnal rhythms of the Grey Seal (Halichoerus grypus). J. Zool., 161(1): 15-23.

Cameron, A.W. 1971. Territorial behaviour in the Western Grey Seal. J. Zool. London, 1964:443-449.

Carrick, R. & S.E. Ingham. 1960. Ecological studies of the Southern Elephant Seal, Mirounga leonina (L.) at Macquarie Island and Heard Island. Mammalia, 24:313-324.

Carrick, R. & S.E. Ingham. 1962. Studies of the Southern Elephant Seal, Mirounga leonina (L.) I. Introduction to the series. CSIRO Wildl. Res., 7(2):85-102.

Carrick, R., S.E. Csordas & S.E. Ingham. 1962. Studies on the Southern Elephant Seal, Mirounga leonina (L.) IV. Breeding and development. CSIRO Wildl. Res., 7(2): 161-168.

Chapsky, K. 1962. Some ecological factors determining seasonal changes in distribution of the White Sea Harp Seal population (Pagophoca groenlandica). Fish. Res. Board Can. Translation Series #380, 1-22.

Cline, D.R., D.B. Sniff & A.W. Erickson. 1971. Underwater copulation of the Weddell Seal. J. Mammal., 52(1): 216-218.

Csordas, S.E. 1958. Breeding of the Fur Seal, Arctocephalus foresteri Lesson, at Macquarie Island. Aust. J. Sci., 21:87-88.

Davies, J.L. 1945. Observations on the Grey Seal (Halichoerus grypus) at Ramsey Island, Pembrokeshire. Proc. Zool. Soc. London, 115:673-694.

Davies, J.L. 1952. Colony size and reproduction in the Grey Seal. Proc. Zool. Soc. London, 122:327-332.

Davydov, A.F. & A.R. Makarova. 1964. Changes in heat regulation and circulation in newborn seals on transition to aquatic form of life. Fiziol. Zh. S.S.S.R., 50(7): 894-898.

Doutt, J.K. 1942. A review of the genus Phoca. Ann. Carnegie Mus., 29:61-127.

Dunbar, M.J. 1949. The Pinnipedia of the Arctic and Subarctic. Fish. Res. Board Can., Bulletin #85, 22pp.

Elsner, R. & D.W. Kenny. 1969. Unpublished observations (1966) in Elsner, R. Cardiovascular adjustment to diving biology of the marine mammals. ed. H.T. Andersen, Biology of the Marine Mammals, New York: Academic Press.

Elsner, R., D. Franklin, R. Critters & D. Kenny. 1966. Cardiovascular defense against asphyxia. Science, 153:941-949.

Fay, F.H. & C. Ray. 1968. Influence of climate on the distribution of walruses, Odobenus rosmarus (L.). I. Evidence from thermoregulatory behaviour, Zoologica, 53(1):1-18.

Feltz, E.T. & F.H. Fay. 1967. Thermal requirements in vitro of epidermal cells from seals. Cryobiology, 3(3): 261-264.

Ferguson, G.A. 1966. Statistical Analysis in Psychology and Education. New York: McGraw-Hill Co. Ltd. 446pp.

Finch, V.A. 1966. Maternal behaviour in the Harbour Seal. Proceedings of the 3rd Annual Conference on Biological Sonar and Diving Mammals, 147-150.

Fiscus, C.H. & G.A. Baines. 1966. Food and feeding of the Stellar and California Sea Lions. J. Mammal., 47: 195-200.

Fisher, H.D. 1950. Seals of the Canadian East coast. Fish. Res. Board Can., 18:1-4.

Fisher, H.D. 1952. The status of the Harbour Seal in British Columbia, with particular reference to the Skeena River. Fish. Res. Board Can. Bull. #93, 58pp.

Fisher, H.D. 1954. Reproduction in the Harp Seal, Fish. Res. Board Can. Rep. #588, 10pp.

Fogden, S.C. 1968. Suckling behaviour in the Grey Seal (Halichoerus grypus) and the Northern Elephant Seal (Mirounga angustirostris). J. Zool. Soc. London, 154: 415-420.

Fogden, S.C. 1971. Mother-young behaviour at Grey Seal breeding beaches. J. Zool. Soc. London, 164:61-71.

Freuchen, P. & F. Salmonsen. 1958. The Arctic Year London: Cape Publ., 440pp.

Harrison, R.J. 1960. Reproduction and reproductive organs in Common Seals, Phoca vitulina, in the Wash East Anglia. Mammalia, 24:372-384.

Harrison, R.J. & G.L. Kooyman. 1966. General physiology of the Pinnipedia. In The Behaviour and Physiology of Pinnipeds. ed. Harrison et al., New York: Appleton-Century-Crofts, 211-296.

Hewer, H.R. 1957. A Hebridean breeding colony of Grey Seals, Halicholerus grypus, (Fab.) with comparative notes on the Grey Seals of Ramsey Island, Pembrokeshire. Proc. Zool. Soc. London, 127:23-68.

Hewer, H.R. 1960. Behaviour of the Grey Seal in the breeding season. Mammalia, 24(3):400-421.

Hewer, H.R. 1964. The determination of age, sexual maturity, longevity and a life-table in the Grey Seal, Halichoerus grypus. Proc. Zool. Soc. London, 142:593-624.

Hewer, H.R. & K.M. Backhouse. 1960. A preliminary account of Grey Seals, Halichoerus grypus (Fab.), in the Southern Inner Hebrides. Proc. Zool. Soc. London, 134(2):157-195.

Hewer, H.R., & K.M. Backhouse. 1959. Field identification of bulls and cows of the Grey Seal, Halichoerus grypus (Fab.). Proc. Zool. Soc. London, 132:641-645.

Imler, R. & H.R. Sarber. 1947. Harbour Seals and Sea Lions in Alaska. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. #28, 22pp.

Irving, L. 1969. Temperature regulation in marine mammals. in The Biology of Marine Mammals, ed. H. Andersen et al., New York: Academic Press.

Irving, L. & J. Hart. 1957. The metabolism and insulation of swine as bare skinned animals. Can. J. Zool., 35: 497-511.

Irving, L., P.F. Scholander & S.W. Grinnel. 1942. The regulation of the arterial blood pressure in the seal during diving. Am. J. Physiol., 135:557-566.

James, P.H.R. 1972. Unpublished data on Sable Island Phoca vitulina.

Kenyon, K.W. 1960. Territorial behaviour and homing in the Alaska Fur Seal. Mammalia, 24(3):432-444.

Kenyon, K.W. 1962. History of the Stellar Sea Lion at the Pribilof Islands, Alaska. J. Mammal., 43(1):68-75.

Kenyon, K.W. & D.W. Rice. 1960. Life history of the Hawaiian Monk Seal. Pac. Sci., 12:215-252.

Kenyon, K.W. & F. Wilke. 1953. Migration of the Northern Fur Seal, Callorhinus ursinus. J. Mammal., 34:86-98.

King, J.E. 1964. Seals of the World. London: British Museum of Natural History, 154pp.

Klinkhart, E.G. 1967. Birth of a Harbour Seal pup. J. Mammal., 48(4):677.

Kooyman, G.L. 1968. An analysis of some behavioural and physiological characteristics related to diving in the Weddell Seal. Antarct. Res. Ser., 11:227-261.

Kooyman, G.L. & H.T. Andersen. 1969. Deep Diving, in The Biology of Marine Mammals. ed. H.T. Anderson, New York: Academic Press, 65-94.

Laws, R.M. 1952. A new method of age determination for mammals. Nature, 169(4310):972-974.

Laws, R.M. 1953. The seals of the Falkland Island and Dependancies. Oryx, 2:87-97.

Laws, R.M. 1956. The Elephant Seal, Mirounga leonina L., II. General social and reproductive behaviour. Falkland Isl. Depend. Surv. Sci. Rep. #13, 1-88.

Laws, R.M. 1962. Age determination of pinnipeds with special reference to growth layers in the teeth. Z. Saugetierk., 27(3):129-146.

Lindsey, A.A. 1938. Notes on the Crabeater Seal. J. Mammal., 19:456-461.

Ling, J.K. 1965. Hair growth and moulting in the Southern Elephant Seal, Mirounga leonina L. in Biology of the Skin and Hair Growth. ed. Lyne & Short, Sydney: Angus and Robertson, 525-544.

Ling, J.K. 1969. A review of ecological factors affecting the annual cycle in island populations of seals. Pac. Sci., 23(4):399-413.

Ling, J.K. 1970. Pelage and moulting in wild mammals with special reference to aquatic forms. Q. Rev. Biol., 45(1):16-54.

Ling, J.K. 1972. Adaptive function of vertebrate molting cycles. Am. Zool., 12:77-93.

Ling, J.K. & C.E. Button. 1973. A preliminary account of Grey Seals and Harbour Seals at St. Pierre and Miquelon. Can. J. Zool. (in press).

Lockley, R.M. 1966. Grey Seal, Common Seal, an account of the Life Histories of British Seals. New York: October House, 175pp.

Lugg, D.J. 1966. Annual cycle of the Weddell Seal in the Vestfold Hills, Antarctica. J. Mammal., 47(2):317-322.

Mansfield, A.W. 1958. The breeding behaviour and reproductive cycle of the Weddell Seal. Scientific Reports, Falkland Isl. Depend. Sur., 18:41pp.

Mansfield, A.W. 1967a. The mammals of Sable Island. Can. Field-Nat., 81(1):40-49.

Mansfield, A.W. 1967b. Seals of arctic and eastern Canada. Fish. Res. Board Can. Bull. #137, 1-35.

Mansfield, A.W. 1966. The Grey Seal in eastern Canadian waters. Can. Audubon, Nov.-Dec.: 161-166.

Mansfield, A.W. & H.D. Fisher. 1960. Age determination in the Harbour Seal, Phoca vitulina. Nature, 186(4718):92.

Mathiesen, O.A. & R.J. Lopp. 1963. Photographic census of the Stellar Sea Lion herds in Alaska, 1956-1958. U.S. Fish. Wildl. Serv., Spec. Sci. Rep., 424, 20pp.

McLaren, I.A. 1958a. The biology of the Ringed Seal (Phoca hispida Schreber) in the eastern Canadian Arctic. Fish. Res. Board of Can. Bull. #118, 97pp.

McLaren, I.A. 1958b. Some aspects of growth and reproduction of the Bearded Seal, Erignathus barbatus Erxleben. J. Fish. Res. Board Can., 15(2):219-227.

McLaren, I.A. 1961a. Methods of determining the numbers and availability of Ringed Seals in the eastern Canadian Arctic. Arctic, 14(3):162-175.

McLaren, I.A. 1961b. Population dynamics and exploitation of seals in the eastern Canadian Arctic. In ed. E. LeCren & Holdgate The Exploitation of Natural Animal Populations. Oxford: Blackwell Science Publ.

Merdsoy, D.(Renouf). 1973. Orientation and navigation of Harbour Seals, Phoca vitulina concolor, in their overland migrations on Sable Island. MSc. Thesis, Memorial University of Newfoundland.

Myers, B.J. 1959. The stomach contents of Harp Seals, Phoca groenlandica Erxleben, from the Magdelene Island, Quebec. Can. J. Zool., 37:378.

Nie, N.H., D.H. Bent & C.H. Hull. 1970. Statistical Package for the Social Sciences. New York: McGraw-Hill Co. Ltd., 343pp.

Nikulin, P.G. 1947. Biological characteristics of the shore aggregations of the Walrus in the Chukotka Peninsula. Fish. Res. Board Can. Transl. Ser. #115, 4pp.

Norris, K.S. & J.H. Prescott. 1961. Observations on the Pacific cetaceans of California and Mexican waters. Univ. Calif. Publ. Zool., 63:291-402.

Olds, J.M. 1950. Notes on the Hood Seal, Cystophora cristata. J. Mammal., 31(4):450-452.

Orr, R.T. 1965. Interspecific behaviour among pinnipeds. Z. Saugertierk., 30:163-171.

Orr, R.T. 1967. The Galapagos Sea Lion. J. Mammal., 48:62-69.

Orr, R.T. & T.C. Poulter. 1965. The pinniped population of Ano Nuevo Island. Proc. Calif. Acad. Sci., 4(32): 377-404.

Orr, R.T. & T.C. Poulter. 1967. Some observations on reproduction, growth and social behaviour in the Stellar Sea Lion. Proc. Calif. Acad. Sci., 35(10): 193-226.

Peters, H.S. & T.D. Burleigh. 1951. Birds of the St. Pierre and Miquelon Islands. Can. Field Nat., 65(5):170-172.

Peterson, R.L. 1966. The Mammals of Eastern Canada. Toronto: Oxford University Press, 465pp.

Peterson, R.S. 1965. Behaviour of the Northern Fur Seal. Dr. Sci. Thesis, Baltimore, Johns Hopkins University.

Peterson, R.S. 1968. Social behaviour in pinnipeds with particular reference to the Northern Fur Seal. In The Behaviour and Physiology of Pinnipeds. ed. Harrison et al., New York: Appleton-Century-Crofts, 3-53.

Peterson, R.S. & G.A. Bartholomew. 1967. Natural history and behaviour of the California Sea Lion. Spec. Publ. Am. Soc. Mammal. #1, 79pp.

Peterson, R.S., C.L. Hubbs, R.L. Gentry & R.L. DeLong. 1968. The Guadalupe Fur Seal: Habitat, behaviour, population size and field identification. J. Mammal., 49(4): 665-675.

Radford, K.W., R.T. Orr & C.L. Hubbs. 1965. The re-establishment of the Northern Elephant Seal, Mirounga angustirostris, off central California. Proc. Calif. Acad. Sci., 31:601-612.

Rakhilin, V.K. 1968. On the biology of the Grey Seal, Halichoerus grypus, Fab. In Investigations Dealing with the Fauna of the Soviet Union. ed. V. Heptner, Moscow State University Publ.

Rand, R.W. 1955. Reproduction in the female Cape Fur Seal. Proc. Zool. Soc. London, 124(4):717-740.

Rand, R.W. 1956. The Cape Fur Seal, Arctocephalus pusillus Schreber. Its general characteristics and moult. Div. Fish. Union South Africa, Invest. Rep. #21.

Rand, R.W. 1959. The Cape Fur Seal, Arctocephalus pusillus Schreber. Distribution, abundance and feeding habits off the southwestern coast of the Cape Province. Div. Fish., Union South Africa, Invest. Rep. #34.

Rand, R.W. 1967. The Cape Fur Seal, Arctocephalus pusillus. General behaviour on land and at sea. Div. Fish., Union South Africa, Invest. Rep. #60.

Rannie, W.F. 1968. Saint-Pierre and Miquelon. 3rd ed. Beamsville, Ontario: Rannie Publications.

Ray, C. & F. Fay. 1968. Influence of climate on the distribution of Walruses, Odobenus rosmarus L. I. Evidence from thermoregulatory behaviour. Zoologica, 53(1):1-18.

Ray, C. & M. Smith. 1968. Thermoregulation of the adult and pup Weddell Seal, Leptonychotes weddelli Lesson, in Antarctica. Zoologica, 53(1):33-48.

Ray, C., W. Watkins & J.J. Burns. 1969. The underwater sound of Erignathus, Bearded Seal. Zoologica, 54(2):79-87.

Ray, C. 1970. Population ecology of Antarctic seals. Antarctic Ecology, vol. 1. New York: Academic Press.

Rust, C.C. 1967. Temperature as a modifying factor in the spring pelage change of short-tailed weasels. J. Mammal., 43:323-328.

Saundby, R.P. 1960. Observations on the Grey Seal at St. Kilda in winter. Proc. Zool. Soc. London, 133:487-490.

Scheffer, V.B. 1958. Seals, Sea Lions and Walruses. A Review of the Pinnipedia. Stanford: Stanford University Press, 179pp.

Scheffer, V.B. & J.W. Slipp. 1944. The Harbour Seal in Washington State. Am. Midl. Nat., 32(2):373-416.

Scholander, P.F. 1940. Experimental investigation on the respiratory functions in diving mammals and birds. Hvalradets Skr., 22:1-131.

Scholander, P.F., L. Irving & S.W. Grinnell. 1942. On the temperature and metabolism of the seal during diving. J. Cell. Comp. Physiol., 21:53-63.

Scholander, P.F. & W.E. Schevill. 1955. Counter-current heat exchange in the fins of whales. J. Appl. Physiol., 8:279.

Scholander, P.F., V. Walters, R. Hock & L. Irving. 1950a. Body insulation of some arctic and tropical mammals and birds. Biol. Bull., 99:225-236.

Scholander, P.F., V. Walters, R. Hock & L. Irving. 1950b. Heat regulation in some arctic and tropical mammals. Biol. Bull, 99:237-258.

Schusterman, R.J. 1968. Experimental laboratory studies of pinniped behaviour. In The Behaviour and Physiology of Pinnipeds. ed. Harrison et al., New York: Appleton-Century-Crofts, 87-171.

Sergeant, D.E. 1951. The status of the Common Seal, Phoca vitulina L., on the east Anglican coast. J. Mar. Biol. Assoc. U. K., 29(3):707-717.

Sergeant, D.E. 1965. Migrations of Harp Seals, Pagophilus groenlandicus Erxleben, in the Northwest Atlantic. J. Fish. Res. Board Can., 22(2):433-464.

Sergeant, D.E. 1973. Feeding, growth and productivity of Northwest Atlantic Harp Seals, Pagophilus groenlandicus. J. Fish. Res. Board Can., 30:17-29.

Siversten, E. 1941. On the biology of the Harp Seal, Phoca groenlandica Erxleben. Hvalradets Skr. Sci. Res. of Mar. Biol. Res., 26:1-178.

Siversten, E. 1953. A review of the family Otariidae. SIV Internat. Zool. Congr. Copenhagen.

Slipjer, E.J. 1962. Whales London: Hutchinson Co. Ltd., 475pp.

Smith, M.S. 1965. Seasonal movements of the Weddell Seal in McMurdo Sound Antarctica. J. Wildl. Manage., 29(3):464-470.

Smith, M.S. 1966. Studies on the Weddell Seal in McMurdo Sound, Antarctica. PhD. Thesis, University of Canterbury, Christchurch, New Zealand.

Sorenson, J.H. 1960. Elephant Seals at Campbell Island. Cape Exped. Ser. Bull. #6, 31pp.

Spalding, D.J. 1964. Comparative feeding habits of the Fur Seal, Sea Lion and Harbour Seal on the British Columbia coast. Fish. Res. Board Can. Bull. #146, 52pp.

Stirling, I. 1969. Population studies on the Weddell Seal. Tuatara (New Zealand), 15:133-141.

Stirling, I. 1970. Observations on the behaviour of the New Zealand Fur Seal, Arctocephalus foresteri. J. Mammal., 51(4):766-778.

Stirling, I. 1971a. Studies on the behaviour of the South Australian Fur Seal, Arctocephalus foresteri Lesson. I. Annual cycle, postures and calls, and adult males during the breeding season. Aust. J. Zool., 19:243-266.

Stirling, I. 1971b. Studies on the behaviour of the South Australian Fur Seal, Arctocephalus foresteri Lesson. II. Adult females and pups. Aust. J. Zool., 19: 267-273.

Stirling, I. & G.L. Kooyman. 1971. The Crabeater Seal, Lobodon carcinophagus, in McMurdo Sound, Antarctica, and the origin of mummified seals. J. Mammal., 52(1):175-180.

Stutz, S.S. 1967. Moult in the Pacific Harbour Seal, Phoca vitulina richardi. J. Fish. Res. Board Can., 24(2):435-441.

Tarasoff, F.J. & H.D. Fisher. 1970. Anatomy of the hind flippers of two species of seals with reference to thermoregulation. Can. J. Zool., 48(4):321-829.

Tavolga, M.C. & F.S. Essapian. 1957. The behaviour of the Bottle-nosed Dolphin Tursiops truncatus. Mating, pregnancy, parturition and mother-infant behaviour. Zoologica, 42:11-31.

Templemen, W., H.J. Squires & A.M. Fleming. 1957. Nematodes in the fillets of cod and other fishes in Newfoundland and neighboring areas. J. Fish. Res. Board Can.,

14(6):831-897.

Terhune, J.M. & K. Ronald. 1972. The Harp Seal, Pagophilus groenlandicus, Erxleben, 1777, III. The underwater audiogram. Can. J. Zool., 50(5): 565-569.

Tuck, L.M. & M.J. Borotra. 1972. Additions to the Avifauna of St. Pierre et Miquelon. Can. Field Nat., 86(3): 279-284.

Van Bemmel, A.C. 1956. Planning a census of the Harbour Seal, Phoca vitulina L., on the coasts of the Netherlands. Beaufortia, 5(54):121-131.

Van Critters, R.L., O.A. Smith, N.W. Watson & D.L. Franklin. 1965. Field study of diving responses in the Northern Elephant Seal. Hvalradets Skr., 48:15-23.

Vas Ferreira, R. 1956. Etologia terrestre de Arctocephalus australis Zimmerman, lobo fino, en las Islas Uruguayas. Trab.Lobos. Mer. Ocean. Pesca, 2:1-22.

Vas Ferreira, R. 1959. Etologia terrestre de Otaria bryonia de Blainville, lobo de un pelo, en las Islas Uruguayas. 1er Congr. Sud am. Zool., La Plata.

Vas Ferreira, R. & E. Palerm. 1961. Efectos de los combios meteorologicos sobre agrupaciones terrestres de Pinnipedios. Trab. Secc. Mammif. Acuat. del Dep. Cien. Tech., 5-19.

Venables, U.M. & L.S. Venables. 1955. Observations on a breeding colony of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London, 125:521-532.

Venables, U.M. & L.S. Venables. 1957. Mating behaviour of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London, 128:387-396.

Venables, U.M. & L.S. Venables. 1959. Vernal coition of the seal Phoca vitulina in Shetland. Proc. Zool. Soc. London, 132(4):665-669.

Waters, W.E. 1965. Grey Seal haulouts at St. Kilda. Proc. Zool. Soc. London, 145:158-160.

White, F.N. & D.K. Odell. 1971. Thermoregulatory behaviour of the Northern Elephant Seal, Mirounga angustirostris. J. Mammal., 52(4):758-774.

Wilke, F. 1954. Seals of Northern Hokkaido. J. Mammal., 35(2):218-224.

Wilke, F. & K.W. Kenyon. 1952. Notes on the food of Fur Seals, Sea Lions and Harbour Porpoises. J. Wildl. Manage., 16(3):396.

Wilke, F. & K.W. Kenyon. 1954. Migration and food of the Northern Fur Seal. Trans. 19th N. Am. Wildl. Conf., 430-440.

Appendix

Table 27

Significant Correlation Coefficients Omitted from the Text.

Variables	Correlation Coefficient
Disturbance & observation hour	rho = .05*
Disturbance & air temperature	rho = .08
Disturbance & sea temperature	rho = .05
Disturbance & wind speed minimum	rho = -.08
Disturbance & wind speed maximum	rho = -.08
Disturbance & cloud cover	rho = -.09
Disturbance & tide height	rho = -.06
Disturbance & tide status	rho = -.09
Disturbance & group span minimum	rho = -.07
Disturbance & group span maximum	rho = -.07
Disturbance & species	rho = -.06
Observation hour & air temperature	rho = -.08
Observation hour & group span minimum	rho = -.06
Observation hour & group span maximum	rho = -.06
Observation hour & haulout rate	rho = -.08
Observation hour & group density	rho = -.07
Air temperature & wind speed minimum	r_{xy} = -.05
Air temperature & wind speed maximum	r_{xy} = -.08
Air temperature & occupied distance	r_{xy} = .05

*P.<.05 for all correlation coefficients.

Table 27 - (Cont'd)

Variable	Correlation coefficient
Sea temperature & cloud cover	$r_{xy} = -.05$
Sea temperature & occupied distance	$r_{xy} = -.06$
Sea temperature & group density	$r_{xy} = .09$
Wind speed minimum & cloud cover	$r_{xy} = .07$
Wind speed minimum & tide height	$r_{xy} = -.08$
Wind speed maximum & tide height	$r_{xy} = -.08$
Cloud cover & tide status	rho = -.05
Cloud cover & haulout location	rho = .06
Cloud cover & group span minimum	$r_{xy} = .05$
Cloud cover & age	rho = .05
Cloud cover & group density	$r_{xy} = -.06$
Tide status & group span minimum	rho = .08
Tide status & group span maximum	rho = .07
Tide status & occupied distance	rho = -.05
Tide height & group number	$r_{xy} = -.08$
Tide height & species	rho = .06
Tide height & age	rho = -.05
Tide height & occupied distance	$r_{xy} = -.07$
Haulout location & group number	rho = -.09
Haulout location & age	rho = -.07
Haulout location & occupied distance	rho = -.09

Table 27 - (Cont'd)

Variable	Correlation coefficient
Group span minimum & group number	r_{xy} = .06
Group span minimum & age	rho = .07
Group span minimum & occupied distance	r_{xy} = -.08
Group number & haulout rate	r_{xy} = .07
Haulout rate & group density	r_{xy} = .08
Tide rate & group density	r_{xy} = -.06